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VARIATIONS IN UROSALPINX

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1. *Introduction.*—In a paper which appeared in 1898 Bumpus[1] showed that, in the case of *Littorina littorea,* an introduced species shows more variability than the same species in its original habitat. This *Littorina* was recently so rare on the Atlantic coast that two pioneer specimens were reported by Verrill from Woods Hole in 1875 while the first specimen found at New Haven was in 1880. Twenty years later it was probably the commonest mollusk to be found along the new England coast and its range extended northward and southward considerably beyond this area. Three lots of 1,000 each, representing the former habitat of the species, were obtained from the coasts of Wales, Scotland and England, respectively, and these shells were measured so as to get an index of their variability. Then ten 1,000-lots of the introduced American shells were collected and measured for comparison and it was found that nowhere in any of the ten different localities, which extended from the St. Croix River in Maine to Newport, R. I., could shells be found that did not have a greater index of variability than did the British shells. Duncker[2] working over

[1] Bumpus, H. C., 1898, "The Variations and Mutations of the Introduced Littorina," *Zool. Bul.*, Vol. I, pp. 247–259.

[2] Duncker, G., 1898, "Bemerkung zu dem Aufsatz von H. C. Bumpus: The Variations and Mutations of the Introduced Littorina," *Biol. Centralbl.*, Bd. 18, pp. 569–573.

Bumpus's data afterwards by the most approved technical methods, confirmed his conclusion.

The oyster-borer, *Urosalpinx cinereus* Say, offers an additional opportunity to test the relative variability of a species when introduced into a new environment as compared with the same species living in the original habitat. This mollusk is a native of the Atlantic coast, living particularly on the oyster beds, where it causes considerable damage. In 1871 Mr. A. Booth, of Chicago, first transplanted the Atlantic oysters to the Pacific coast where, with varying success, they have since been maintained. Two lots of these shells were obtained from the San Francisco beds in 1898 and it was the original purpose of this paper to compare these introduced California shells with individuals from the Atlantic coast whence they were emigrated.

The work was principally done at the Woods Hole research laboratory of the U. S. Fisheries Bureau and I wish hereby to acknowledge the many courtesies received from the officers connected with that bureau, and particularly to express my indebtedness to Professor Bumpus who suggested the original problem. I wish also here to thank the following persons for aid in obtaining specimens: Dr. Bumpus for 1,500 California shells; Dr. H. M. Smith for 1,700 from Prince's Bay, Staten Island; Mr. G. W. Hunter, for 1,000 from Norwalk Harbor, Ct.; Miss M. E. Smallwood for 1,000 from Cold Spring Harbor, Long Island; Mr. C. T. Brues and Mr. A. L. Melander for 8,000 from Woods Hole, Mass., in 1902 and 1903; and Mr. C. S. Bennett for 4,000 from Woods Hole in 1908. Finally, I am particularly under obligation to Dr. J. Arthur Harris, who very kindly passed the manuscript under his statistical eye. It should be added that while Dr. Harris is responsible for much that does not appear he is in no way committed to what remains.

2. *Methods.*—In collecting, only living specimens were taken, thus eliminating beach-worn shells, and collecting was always done " systematically at random" (Daven-

port) so that any lot would, as far as possible, be typically representative of its locality. Lots of 1,000 were taken and shells not immediately measured were simply preserved in formalin until opportunity for making use of them arose.

In ascertaining statistically the variability of any lot of shells it was necessary to select for measurement two easily definable dimensions common to every shell and take the ratio of these two dimensions for reasons which will directly appear. The dimensions selected were the total height of the shell (*a* to *b*, Fig. 1) and the greatest dimension of the shell-aperture (*a* to *c*, Fig. 1). It was possible to determine these standards on *Urosalpinx* by the use of calipers with a considerable degree of accuracy. Any other dimensions which would lend themselves equally well to accurate measurement would have served quite as well to establish a criterion from which a comparison of variability in different lots of shells could be computed, since it was the *fact* of variation, and not the direction or character of it that was the object of the inquiry.

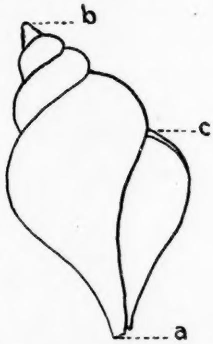

FIG. 1. a–b = height of shell, a–c = greatest mouth aperture.

The ratio of the two dimensions was used instead of a single dimension in order to eliminate as far as possible heterogeneity referable directly to growth. Had height alone, for instance, been used then groups of shells would be related to each other with reference to their variations in size or age only, and all that could be said in comparing lots from two localities would be that those in one locality averaged taller or shorter, and presumably, therefore, were older or younger than those from another locality. This would not be a suitable index for variation in form. On the other hand, when the ratio of two dimensions is taken, then the factor of absolute

size is eliminated, while the factor of form remains. Thus a shell 20 mm. high with a greatest shell-aperture of 12 mm. would fall in the 60 per cent. class (20 : 12 = 60 per cent.), as would also a smaller shell 15 mm. high with a greatest shell aperture of 9 mm. (15 : 9 = 60 per cent.), while shells of the same height as the first, but with a 14 mm. greatest shell aperture, would rightly represent a variation in form since they fall into a different (70 per cent.) class (20 : 14 = 70 per cent.). This distinction may be more apparent by reference to Fig. 2 where

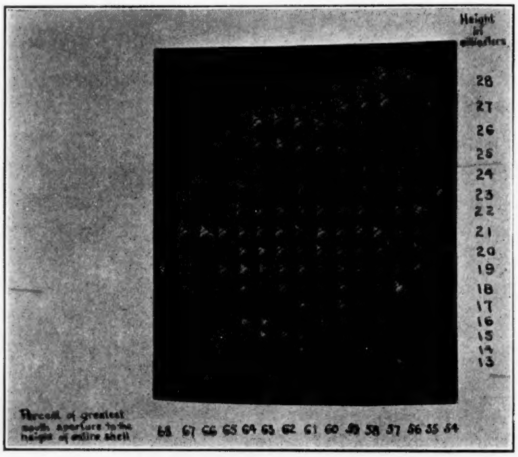

FIG. 2. The different classes of variants occurring in a specimen lot of one thousand shells to show how size, or the factor of growth, was eliminated in classifying the variants. The shells in the vertical lines all in the *same* percentage class, although their size (height) differs. The shells in the horizontal lines are in *different* percentage classes, although their size (height) is alike.

single representatives of all the different classes of variants that appeared in a certain thousand-lot of shells are arranged to show this point. Here the shells in any horizontal row are the same height, and have, therefore, presumably reached the same stage of growth, but at the same time they are all unlike in form since those at the left have larger "greatest shell apertures" than those at the right. On the contrary, all the shells in any vertical

row, although varying in size, fall into a single form-group as determined by the ratio between total height and the greatest shell-aperture. A measuring machine such as that used by Bumpus for his work on *Littorina* made it possible to read the ratio of the two dimensions directly from a graduated arm without trouble of computation, thus greatly lessening the tediousness in obtaining the data.

3. *Are Variation Curves of any Locality Distinctive for that Locality?*—Tests were first made to ascertain how far the personal element in making the measurements could affect the results, since judgment in the use of calipers and in the manipulation of the measuring machine are by no means invariable factors. One such test, which is typical of several which were made, is shown in Table I, where the same lot of shells was twice measured.

TABLE I

THE SAME LOT OF A THOUSAND SHELLS TWICE MEASURED TO SHOW AMOUNT OF ERROR IN MANIPULATION.

Percentage Class.	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	Arithmetical Mean.	Standard[3] Deviation.	Probable[3] Error.
First measuring	1	2	2	5	28	58	118	185	182	171	139	49	38	15	5	2	62.101	1.992	±.0300
Second measuring		2	2	4	25	66	128	182	179	176	120	59	33	18	4	2	62.071	2.088	±.0314
																Difference	.030	.096	

The numbers ought to be identical. Their deviation from exact similarity represents the imperfections of manipulation and it will be seen that according to this test a difference of .096 in the standard deviation with a probable error of about ± .03 may be regarded due to imperfect technique.

Now in order to test whether the variation is characteristic and constant for any locality whence the shells came, two 1,000-lots were gathered on the same day in 1898 from the same restricted group of rocks on Nobska Point, Woods Hole, by no means thereby exhausting the

supply. The figures for these two lots are shown together in Table II.

TABLE II

TWO LOTS OF SHELLS OF ONE THOUSAND EACH TAKEN FROM THE SAME ROCKS AT THE SAME TIME TO SHOW THE PROBABLE VALIDITY OF PLACE-MODES.

Percentage Class.	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	A. M.	σ	P. E.
First lot		2	3	20	40	80	150	149	196	157	112	57	21	10	4	1	61.737	2.152	.0323
Second lot	2	2	31	14	61	79	144	148	185	160	106	55	25	10	7		61.694	2.234	.0336
Difference																	.043	.082	

The close resemblance of these two lots, which show a difference in standard deviation (.082) less than that shown when the same lot is measured twice (.096) as just indicated in Table I, warranted confidence in the probability that all the shells from a given place, when collected at the same time, exhibit the same characteristic sort of variation which may therefore be regarded as distinctive for that particular locality. Furthermore, a glance at Table III will show how widely the shells of various localities may differ with regard to the character and degree of their variability, a fact that assures us that in *Urosalpinx* we are dealing with a form whose variation is considerable enough to furnish favorable material for quantitative treatment.

[3] Formulas for standard deviation and probable error of standard deviation are found in Davenport's Statistical Methods (Davenport, C. B., 1899), as follows:

$$\text{Standard deviation} = \frac{\text{Sum of} \sqrt{[(\text{deviation of class from mean})^2 \times \text{frequency of class}]}}{\text{Number of variates}} \quad \text{or} \quad \frac{\Sigma\sqrt{(x^2 \cdot f)}}{n}$$

$$\text{Probable error of standard deviation} = \pm 0.6745 \frac{\text{Standard deviation}}{\sqrt{2} \times \text{number of variates}} \text{ or P. E.} = \pm 0.6745 \frac{\sigma}{\sqrt{2n}}$$

TABLE III

Two Lots of Shells of One Thousand Each to Show Extremes of Variation.

Percentage Class.	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Devil's Foot	1	0	2	6	22	38	99	144	193	217	163	73	25	14
Prince's Bay						4	5	9	36	45	65	79	132	84

Percentage Class.	64	65	66	67	68	69	70	71	72	73	A. M.	σ	P. E.
Devil's Foot	3										58.358	1.849	.0279
Prince's Bay	83	117	75	88	83	42	33	15	2	1	63.976	3.407	.0514
									Difference		5.618	1.558	

4. *A Comparison of Atlantic with Pacific Shells.*—In the summer of 1898, following the method employed by Bumpus with *Littorina,* 7,006 *Urosalpinx* shells from various localities near Woods Hole were obtained and measured, with which were compared 1,528 introduced shells from two localities in California. From Table IV, in which these data are brought together, it will be seen that Bumpus's work on *Littorina* is apparently confirmed, that is, there is more variability in the introduced than in the endemic form, although the margin of probable error permits an overlapping in some instances.

TABLE IV

Atlantic and Pacific Shells Compared.

Locality.		Number of Shells.	A. M.	σ	P. E.
Woods Hole	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	1,002	61.737	2.152	±.0324
	Nobska Point	1,001	61.944	2.234	±.0337
	Nobska Point	496	66.944	2.366	±.0507
	Barnacle Beach	998	63.932	2.604	±.0393
	Big Wepecket	1,006	57.426	2.052	±.0308
	Mid Wepecket	500	57.606	2.098	±.0447
Average			61.066	2.335	±.0386
California	Belmont Beds	1,008	59.051	3.023	±.0454
	San Francisco Bay	220	60.892	3.361	±.0703
Average			59.664	3.138	±.0538
Difference				.803	

5. *Shells from Buzzard's Bay and Vineyard Sound Compared.*—For the sake of scientific peace of mind the

incident should have been closed at this point, but uncertainty as to the degree in which the element of time took part in influencing the place-modes of variability led to the examination during the following summer of several thousand more shells. Four convenient localities near Woods Hole (see Fig. 3) where *Urosalpinx* was abundant were selected and three lots of 1,000 each were collected from each of these localities at intervals of two weeks apart. The data obtained from these shells is arranged in Table V.

TABLE V

WOODS HOLE SHELLS ARRANGED TO SHOW PLACE VARIATION AFTER TWO WEEKS INTERVALS OF TIME.

Locality.		Time when Collected.	Number of Shells.	A. M.	σ	P. E.
Buzzard's Bay	West Shore	July 5	1,000	58.669	2.137	±.0322
		July 21	1,000	59.598	2.211	±.0333
		Aug. 5	920	60.308	2.211	±.0323
		Average		59.503		
	Penzance Point	July 5	986	58.458	2.137	±.0304
		July 21	1,000	58.030	2.135	±.0322
		Aug. 5	1,000	60.308	1.982	±.0323
		Average		58.888		
Vineyard Sound	Nobska Point	July 5	1,000	62.085	2.040	±.0307
		July 21	1,000	62.690	2.172	±.0327
		Aug. 5	1,005	64.022	2.312	±.0347
		Average		62.934		
	Barnacle Beach	July 5	1,036	60.978	2.093	±.0310
		July 21	1,001	61.925	2.119	±.0319
		Aug. 5	1,001	63.281	2.186	±.0329
		Average		62.048		

From Table V it will be seen that in each of the four localities the arithmetical mean (A.M.) increased steadily, except for the Penzance Point—July 21—lot of shells. This general increase may be due to the fact that, as the season advanced, there were fewer young shells in any 1,000 lot. The young are produced in May and June from individuals that have wintered over, so that early in July the *Urosalpinx* community is made up of old adults from the preceding year and of young of various sizes. A month later the population is more uniform,

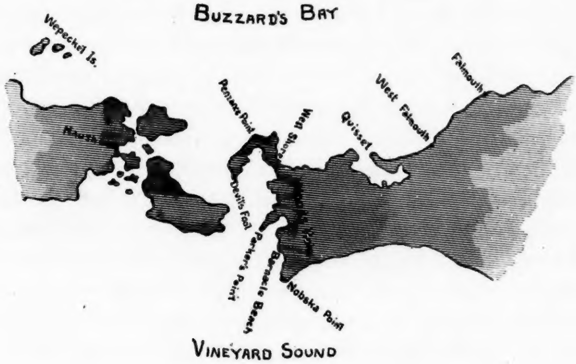

FIG. 3.

due to the rapid growth and approaching maturity of the young ones. That the ratio of the two dimensions used changes somewhat with age is shown in a later table (Table VII), a fact that somewhat complicates a comparison between shells of any two localities. It will furthermore be observed that the variability of the Vineyard Sound shells as indicated by their standard deviation increases steadily from July 5 to August 5, reaching its maximum upon the latter date, but that for both the Buzzard's Bay localities the same is not true; on the contrary, in the case of Penzance Point the August 5 collections showed the *least* variability of any time. The fact that the maximum of the shifting seasonal variation does not occur at the same time in localities almost within sight of each other, as in the present instance, plainly indicates that comparisons of variabilities based upon the time-factor alone do not take everything into consideration. The shells from Buzzard's Bay range in their arithmetical mean from 58.030 to 60.308 while those from Vineyard Sound, separated from the former only by the narrow tongue of land on which the village of Woods Hole is located, form a distinct class ranging from 60.978 to 64.022. Here is a distinct place difference in the shells of the two general localities in question.

Shells obtained from other localities in Buzzard's Bay

and Vineyard Sound conform quite closely with respect to their arithmetical means to the standards above mentioned.

6. *Time and Place Factors Compared.*—When a comparison of the standard deviation of these 1899 shells is made to ascertain whether the greater variability is associated with time (due to inherent germinal modifications), or with place (associated with environmental modifications), it appears that while time is rather the more important factor, yet the result is not uniform and convincing. This comparison is shown in Table VI, in which the difference between the standard deviation of the July shells of each locality with the July 5 shells of three other localities is obtained to indicate differences due to place, and second, the difference between standard deviation of the July 5 shells in each locality and those of July 21 and August 5 for the corresponding locality are reckoned to show the effect of time.

TABLE VI

A COMPARISON OF THE DIFFERENCES IN THE STANDARD DEVIATION VARIABILITY OF THE 1899 WOODS HOLE SHELLS ARRANGED ACCORDING TO THE PLACE-FACTOR AND THE TIME-FACTOR.

Place Differences (July 5).				Time Differences.		
Nobska Point.	West Shore.	Penzance Point.	Barnacle Beach.	July 5.	July 21.	August 5.
—	.097	.025	.053	Nobska Point	.132	.272
.097	—	.122	.044	West Shore	.074	.080
.025	.122	—	.078	Penzance Point	.120	.033
.053	.044	.078	—	Penzance Beach	.026	.093
.058	.088	.075	.058	Average	.088	.119

In Table VI, if we first consider the case of the Nobska Point shells in the top line of the table and utilize those collected upon July 5 as a standard for comparison it appears that shells from the same locality but collected two and four weeks later show a greater difference in variability (standard deviation) than shells collected from any of the three other neighboring localities upon the same date of July 5. That is, the factors dependent upon time

play a greater part in determining the amount of variability than do the factors dependent upon place. Furthermore, there is a greater difference of variability after four weeks (.272) than after two weeks (.132) have elapsed, just as would be expected if a progressive time change is taking place. The same general result appears also when an average of the four localities is reckoned, as shown in the bottom line of the table, but an examination of the second, third and fourth lines of the table reveals several instances in detail of non-conformity to this apparently general conclusion that time has more to do with determining variability than place. It is apparently safe to conclude, however, that the factors dependent upon time are at least as important, if not demonstrably more so, than those dependent upon space or locality.

TABLE VII

WOODS HOLE SHELLS ARRANGED ACCORDING TO THEIR SIZE.

Height in mm.	Actual No. of Shells.	A. M. Per Cent.	σ	P. E.
11	96	64.070	3.487	± .1753
12	139	63.911	3.558	± .1445
13	252	63.372	3.465	± .1049
14	341	62.983	3.954	± .1029
15	524	62.940	3.602	± .0755
16	866	61.960	3.020	± .0489
17	1,296	61.595	3.146	± .0417
18	2,033	61.171	3.124	± .0325
19	2,328	60.913	3.143	± .0311
20	3,366	61.004	3.209	± .0227
21	4,404	60.914	3.056	± .0219
22	4,807	60.739	3.122	± .0213
23	3,836	60.507	2.881	± .0222
24	2,854	60.171	2.951	± .0276
25	1,782	59.856	2.943	± .0322
26	949	59.706	2.663	± .0412
27	539	59.520	2.704	± .0555
28	239	59.213	2.520	± .0777
29	109	59.654	2.907	± .1328
30	63	59.305	2.740	± .1646
31	30	58.334	2.182	± .2455
32	23	58.665	1.916	± .1905
33	6	58.332	4.015	± .7818
34	12	59.083	3.009	± .4141
35	5	57.600	2.059	± .4392
36	3	60.000	8.185	±2.2554
37	1	54.000		
Total	30,903			

7. *Variations due to Age.*—It is indeed true that as the snail grows older not only is there a change in the total height of the shell, as would be expected, but also the ratio of the largest shell-aperture to the height diminishes in a definite way and the standard deviation becomes generally less. In other words, the older the shell becomes the less is the relative size of the largest shell-aperture to the total height and the less does it tend to deviate from the arithmetical mean. In Table VII the total number of shells measured in 1898, 1899, 1900 are arranged according to their height to illustrate this fact.

8. *Staten Island and California Shells Compared.*—In 1900 shells were obtained from several additional localities, among which were 1,665 from oyster beds on Prince's Bay, Staten Island. This lot of shells has a special interest because it was from this particular locality, according to Dr. H. M. Smith, of the U. S. Fish Commission, that the oysters, and accidentally with them the *Urosalpinx,* were obtained for transplanting to San Francisco in 1871. A comparison of the Staten Island shells with the California shells appears in Table VIII.

TABLE VIII

A COMPARISON OF CALIFORNIA SHELLS WITH THOSE FROM STATEN ISLAND.

	No.	A. M.	σ	P. E.
California	1,528	59.741	3.286	$\pm .0398$
Staten Island	1,664	63.166	3.508	$\pm .0412$

From this table one of three conclusions must be drawn: (1) That the introduced California shells vary less in their new environment than they did in the place they came from or (2) that the Staten Island shells have increased remarkably in their variability since 1871, or (3) that place-modes in which time element is not known are of little value in working with organisms of this kind.

9. *Shells of Successive Years Compared.*—Further-

more, the analysis of the 1899 shells indicates that a proper comparison of place-modes of variability could be made only on material of the same relative age, which presumably could be approximated best by collecting the shells in neighboring localities at the same time or in any one locality at the same time in successive years. Consequently lots of 1,000 shells from each of the four Woods Hole localities mentioned in Table V were collected during the first week of August, with some omissions, for several years. These data are assembled in Tables IX and X.

In Table IX it is made apparent that, when the time element is reduced to a minimum by comparing only August 5 shells of various years, the shells of Buzzard's Bay (West Shore and Penzance Point) fall into a group distinct from those of Vineyard Sound (Nobska Point and Barnacle Beach), at least so far as the A. M. is concerned. The A. M. of 11,476 Buzzard's Bay—August 5 shells is 61.330 while the A. M. for 14,503 Vineyard Sound—August 5 shells, is 64.303. In no individual lot of Buzzard's Bay shells does the A. M. reach as high as the Vineyard Sound average and in no one lot of the Vineyard Sound shells does the A. M. fall as low as the Buzzard's Bay average of 61.330.

The standard deviation of the August shells shows no decided grouping with reference to Buzzard's Bay and Vineyard Sound, although those from the latter locality show a slightly higher total average which is probably quite without significance. In general, then, it may be said that during the first week of August the Buzzard's Bay shells show a lower ratio of greatest shell-aperture to height (and consequently may be regarded as rather more advanced in their life cycle) than those of Vineyard Sound, but that they present no significant difference in variability.

In each of the two general localities which were more exposed to the open water and the beat of the waves, viz., Nobska Point and Penzance Point, is the variabil-

TABLE IX

A COMPARISON OF AUGUST SHELLS OF VARIOUS YEARS TO SHOW PLACE-VARIATION.

Place.		Time.	Number.	A. M.	σ	P. E.
Buzzard's Bay	West Shore	1898	1,001	58.928	2.339	±.0352
		1899	920	60.308	2.057	±.0323
		1900	405	60.711	2.042	±.0484
		1901	—	—	—	—
		1902	1,000	63.251	3.280	±.0491
		1903	1,000	61.419	2.234	±.0336
		1904	—	—	—	—
		1905	1,000	61.086	2.012	±.0303
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	60.380	2.469	±.0372
	Total		6,326	60.890	2.663	±.0160
	Penzance Point	1898	1,002	61.718	2.737	±.0412
		1899	1,000	60.170	1.982	±.0299
		1900	1,001	60.617	2.008	±.0316
		1901	—	—	—	—
		1902	1,000	64.155	2.938	±.0443
		1903	1,000	62.773	2.086	±.0314
		1904	—	—	—	—
		1905	1,000	61.381	1.970	±.0775
		1906	—	—	—	—
		1907		Too scarce	to collect	
		1908	—	—	—	—
	Total		5,150	61.870	2.814	±.0187
Total for Buzzard's Bay			11,476	61.330	2.805	±.0125
Vineyard Sound	Nobska Point	1898	2,498	62.751	3.041	±.0290
		1899	1,005	64.022	2.312	±.0347
		1900	1,000	66.396	2.449	±.0369
		1901	—	—	—	—
		1902	1,000	66.775	2.707	±.0407
		1903	1,000	64.605	2.128	±.0321
		1904	—	—	—	—
		1905	1,000	63.765	2.653	±.0400
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	63.296	2.719	±.0410
	Total		8,503	64.205	3.048	±.0158
	Barnacle Beach	1898	998	63.942	2.604	±.0393
		1899	1,000	63.281	2.186	±.0329
		1900	1,000	66.798	2.052	±.0309
		1901	—	—	—	—
		1902	1,002	66.085	2.351	±.0354
		1903	1,000	63.526	2.546	±.0383
		1904	—	—	—	—
		1905		Too scarce	to collect	
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	63.017	2.300	±.0347
	Total		6,000	64.442	2.602	±.0160
Total for Vineyard Sound			14,503	64.303	2.865	±.0113

ity (standard deviation) greater than at West Shore and Barnacle Beach, respectively, which were somewhat more sheltered situations.

Turning to Table X, where the August shells are grouped by years rather than by localities, the A. M. is seen to fluctuate with considerable regularity, reaching in 1902 the highest average ratio. It seems not improb-

TABLE X

August Shells Grouped to Show Yearly Variation.

Year.	Locality.	No.	A. M.	σ	P. E.
1898	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	2,498	62.751	3.041	±.0290
	Barnacle Beach	998	63.942	2.604	±.0393
	Average	(5,499)	61.899	3.389	±.0218
1899	West Shore	920	60.308	2.057	±.0323
	Penzance Point	1,000	61.170	1.982	±.0299
	Nobska Point	1,005	64.022	2.312	±.0347
	Barnacle Beach	1,000	63.281	2.186	±.0329
	Average	(3,925)	61.981	2.649	±.0202
1900	West Shore	405	60.711	2.042	±.0484
	Penzance Point	1,001	60.617	2.098	±.0316
	Nobska Point	1,000	66.396	2.449	±.0369
	Barnacle Beach	1,000	66.798	2.052	±.0309
	Average	(3,406)	64.139	3.459	±.0281
1902	West Shore	1,000	63.251	3.280	±.0491
	Penzance Point	1,000	64.155	2.938	±.0443
	Nobska Point	1,000	66.775	2.707	±.0407
	Barnacle Beach	1,002	66.085	2.351	±.0354
	Average	(4,002)	65.067	3.012	±.0227
1903	West Shore	1,000	61.419	2.234	±.0336
	Penzance Point	1,000	62.773	2.084	±.0314
	Nobska Point	1,000	64.615	2.128	±.0321
	Barnacle Beach	1,000	63.526	2.546	±.0383
	Average	(4,000)	63.083	2.542	±.0291
1905	West Shore	1,000	61.086	2.012	±.0303
	Penzance Point	149	61.381	1.970	±.0775
	Nobska Point	1,000	63.765	2.653	±.0400
	Barnacle Beach	—	—	—	—
	Average	(2,147)	62.077	2.718	±.0280
1908	West Shore	1,000	60.380	2.469	±.0372
	Penzance Point	—	—	—	—
	Nobska Point	1,000	63.296	2.719	±.0410
	Barnacle Beach	1,000	63.017	2.300	±.0347
	Average	(3,000)	62.321	2.802	±.0244

able that the missing year 1901 would have furnished a higher maximum than 1902, and that in some future year the high average of 1902 may again be attained.

10. *Dense and Sparse Population Compared.*—Two lots of shells collected in 1899 deserve a separate paragraph. They represent the extremes among all the lots collected with respect to the density of the population. They came from localities on the eastern shore of Buzzard's Bay about five miles apart and were collected during the same week.

TABLE XI

	No.	A. M.	σ	P. E.
Quisset-to-West-Shore	862	60.464	3.127	$\pm .0507$
West Falmouth	1,000	59.091	1.913	$\pm .0297$

The Quisset-to-West-Shore lot was gathered over an area extending fully a mile along the rocky shore and they were so scarce that it was necessary to utilize the low-tide period of two successive days in order to obtain them, and even then only 862 were obtained instead of the usual 1,000. The West Falmouth lot, on the contrary, were all taken within a few minutes from a single rock about five feet in diameter without by any means exhausting the supply.

It may be that the latter, as would be inferred by their proximity, were more closely related to each other than were the former, and consequently they might be expected to present less variation, or it is possible that the Quisset-to-West Shore lot—representing the pioneers or survivors in an apparently inhospitable area—succeeded in maintaining themselves because of their greater variability (*i. e.*, adaptability). Certain it is, at any rate, that they represent the greatest variability (standard deviation) of any lot of shells obtained from the Atlantic coast except a thousand from West Shore in August, 1902, and those already mentioned from Staten Island.

11. *Variation of the Species Urosalpinx as a Whole.* —By combining the data of all the shells measured—a

total of 50,424—it is possible to approximate a measure of the variability of *Urosalpinx as a species* much more nearly than is possible with smaller lots of 1,000. Such a combination is shown in Table XII, which will be seen to furnish the figures for a curve of considerable regularity in which the arithmetical mean is 61.662 and the standard deviation is 3.367±.0071. This standard deviation is exceeded in but a single instance among the smaller lots which make it up—namely, in the 1,664 shells from Staten Island which show a standard deviation of 3.508±.0412.

TABLE XII

Per Cent.	50	51	52	53	54	55	56	57	58
No.	4	15	32	120	289	675	1,510	2,450	3,812
Per Cent.	59	60	61	62	63	64	65	66	67
No.	5,052	5,491	5,861	5,515	5,115	4,225	3,647	2,357	1,714
Per Cent.	68	69	70	71	72	73	74	75	76
No.	1,161	737	373	181	54	21	8	4	1

A. M., 61.662. σ, 3.367. P. E., ±.007. Total No., 50,424.

12. *Summary.*—1. When two lots of 1,000 *Urosalpinx* shells each are taken from the same locality they resemble each other sufficiently to indicate a character typical for the locality.

2. Lots of shells from different localities vary widely enough from each other to be easily distinguished, indicating thereby that the varying environment associated with different localities exerts a measurable effect.

3. Endemic Atlantic shells (with one exception noted below) vary less than shells introduced into a new environment (California).

4. The shells of Buzzard's Bay have a lower ratio of greater shell-aperture to shell-height than those of Vineyard Sound.

5. When shells from the same localities in successive fortnights are compared there is an increase in the ratio of greater shell-aperture to shell-height (A. M.) and also a slight increase in variability as shown by the standard deviation, except in the case of the shells from Penzance Point.

6. When growth which we detect by taking into consideration the *time*-factor is compared with the environmental factors that depend upon *place,* the former apparently plays the greater rôle in causing variations.

7. As *Urosalpinx* grows larger (older) the ratio of its greatest shell-aperture to its height diminishes with regularity and its standard deviation tends to become somewhat less.

8. Shells from Staten Island whence the introduced California shells were originally derived show greater variability than the California shells.

9. When the August shells of successive years from the same localities are compared the A. M. of the ratio between the greater shell-aperture and shell-height fluctuates with noticeable regularity, reaching a maximum in 1902.

10. Shells from the localities more exposed to the beat of the waves show greater variability than those from the more protected places.

11. When dense and sparse populations are compared the dense population shows less variability.

12. The average mean of the ratio of greater shell-aperture to height of shell for 50,424 *Urosalpinx* shells is 61.662. The standard deviation is $3.367 \pm .0071$.

13. *Conclusion.*—So far as the statistical method is able to reveal, it is extremely doubtful whether or not *Urosalpinx* when introduced into a new habitat exhibits greater variability than when in its native habitat. The change in the variability appearing in successive fortnights in shells from the same locality as well as in change showing itself in the August shells from the same locality in successive years is marked enough to indicate plainly the working of an ontogenetic variability independent of environmental modification, that is, a *time*-factor as distinguished from a *place*-factor. In consequence of this it is practically impossible to collect homologous lots of individuals of these shells upon which the place- (or environmental-) factor may be accurately determined.

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN GYMNOSPERMS[1]

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To the cytologist the most interesting phases of a plant's life history are fertilization and the reduction of chromosomes, processes which initiate the sporophyte and gametophyte generations and which are of the utmost importance in any cytological theories of heredity.

We shall not attempt to define fertilization, but shall simply state that, in our opinion, the process is essentially uniform from its first appearance in the fusion of equal gametes in the lower algæ, up to the heterogamy of the angiosperms and, in our opinion, this fusion of gametes, whether they be the equal gametes of the lower algæ or the unequal gametes of the higher plants, always initiates a sporophytic phase in the life history, a phase which normally continues until the reduction of chromosomes brings it to a close and initiates the gametophytic phase.

The gymnosperms have as yet only a single well-established case of apogamy and not even a single case of apospory, and, consequently, their only mode of reproduction, aside from occasional budding, is that resulting from fertilization.

Since the significance of fertilization becomes more intelligible with increasing knowledge of the participating gametes, it is of prime importance to know the structure, evolution and behavior of the sperms and eggs.

SPERMATOGENESIS

The sperms of fossil gymnosperms are almost unknown, but it is safe to say that Cycadofilicales and

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Cordaitales had swimming sperms, and further, that they had no pollen tubes, the pollen grains reaching the female gametophyte directly, then discharging their sperms about as in the living heterosporous Pteridophytes.

Definite knowledge of the structure of the sperm begins with the cycads, where the sperms are so large that they are easily visible to the naked eye. Broadly speaking, their development is like that of most pteridophytes. In the most thoroughly investigated fern, after the spermatogenous divisions have ceased, two blepharoplasts appear in each cell, which then divides so that each of the two resulting cells contains one nucleus and one blepharoplast. From the blepharoplast there is developed a more or less spiral band which gives rise to numerous cilia.

In gymnosperms, with the exception of *Microcycas, Cupressus* and occasionally, *Ceratozamia,* no spermatogenous divisions precede the formation of the cell which is to produce the pair of sperms, and in these three genera it is not known whether the blepharoplast appears any earlier than in the pteridophytes. I suspect that it does not, but it is certain that in the cycads and in *Ginkgo* two blepharoplasts always appear in the body cell which is to produce the pair of sperms, and while the blepharoplasts are at first very inconspicuous, they finally become larger than the nuclei of most angiosperms.

The mature sperm of the cycad consists of a very large nucleus surrounded by a thin layer of cytoplasm in which is imbedded the spiral band with its thousands of cilia. Compared with the sperms of the pteridophytes, the sperms of the cycads are immensely larger and much less numerous. It must be a fact of some significance that the living gymnosperms, with two or three exceptions, have only two sperms, for the production of sperms in pairs is universal from the liverworts to the orchids. Whether the production of sperms in pairs is associated with a separation of sexes is not

known. Objections to such a suggestion are easily raised, but the question seems worth investigation, especially since little is known of the behavior of the chromatin during the mitosis by which two sperms are produced from the body cell.

Except in the cycads and *Ginkgo,* there are no motile sperms in living gymnosperms, but, in our opinion, the transition is not so abrupt as some writers believe. The definitely organized male cells of such genera as *Sequoia* and *Thuja* look very much like the young sperms of a cycad immediately after the division of the body cell, the principal difference being the absence of the blepharoplast, which is such a conspicuous feature in the development of the sperms of cycads and *Ginkgo.* In regard to the several genera with well-organized male cells, the statement is made that there are no structures which could be interpreted as the vestiges of blepharoplasts, but the figures accompanying the various accounts are not convincing and it seems entirely possible that vestiges may yet be found.

According to all the accounts, either as expressed in the text or to be inferred from the figures, the body cell in Taxeæ, Taxodieæ and Cupresseæ gives rise directly to the male cells, there being no formation of sperms within sperm mother-cells. The accounts may be correct, but it must be remembered that a competent observer described just such a condition in one of the cycads, where it is now known that the sperms are formed within sperm mother-cells from which they are afterwards discharged. Among the Coniferales, the well-organized male cell is found in the Taxaceæ, Taxodieæ and Cupresseæ.

In the rest of the Coniferales, which means the Araucarieæ and Abieteæ, there are no organized male cells, but only male nuclei lying free in the cytoplasm of the body cell, and this cytoplasm not always sharply limited from that of the pollen tube. Accompanying these male nuclei there are often structures which might be interpreted as the vestiges of blepharoplasts. According to some observers, one of the male nuclei is smaller than the

other, possibly indicating the future elimination of the smaller nucleus.

That both the male cell of *Thuja* and the male nucleus of *Pinus* are descendants of swimming sperms is not to be doubted. The male cell of *Thuja* has lost its cilia and, perhaps, is no longer formed within a parent cell, while *Pinus* has gone further and no longer organizes a definite male cell. In this respect, the *Pinus* gametophyte is more widely separated from the ancestral form than is the gametophyte of *Thuja*.

In some genera, like *Torreya* and *Taxus,* the reduction has proceeded in another direction, two male cells being retained, but one of them having become much smaller than the other and having ceased to function, indicating its future elimination.

It is interesting to note that in Coniferales, with the exception of the Podocarpeæ, those forms with definitely organized male cells have no prothallial cells in the pollen grains, while those with the free male nuclei have retained more or less of the ancestral prothallium; *e. g.*, *Pinus* has retained the prothallial cells, but no longer organizes a definite male cell, while *Thuja* has retained the definitely organized male cell, but has lost the prothallial cells. And further, those genera which have retained the definitely organized male cell no longer organize a definite ventral canal cell, having lost the wall between the ventral canal nucleus and that of the egg, a step toward the complete elimination of even a ventral canal nucleus. Whether there are any causal relations among these reductions is not obvious, but it is interesting to note the correlation. If all evolutionary lines would only progress at the same pace, or if we could discover causal relations between the lines, it would facilitate the construction of phylogenies.

Oogenesis

We have seen that in spermatogenesis the gymnosperms show a reduction series from the highly differentiated motile sperms of cycads to the free male nuclei

of *Pinus*. Oogenesis does not cover so great a range, for motile eggs are not found above the thallophytes. In its most primitive condition, the archegonium of the gymnosperms is more reduced than any found in pteridophytes, for there is no neck canal cell. An egg with a definite ventral canal cell, as in *Ginkgo* and *Pinus,* is the most primitive condition found in gymnosperms. Beyond this there is the elimination of the wall between the ventral canal nucleus and that of the egg, as in cycads and many conifers, a natural step in the elimination of the ventral canal nucleus, and in *Torreya,* even the nuclear division has probably failed to take place, so that the central cell functions directly as an egg. A still further reduction is found in *Tumboa* where the incomplete septation of the female gametophyte results in a failure to organize a definite egg; and finally, there is a complete suppression of any septation whatever, so that the egg is represented only by a nucleus with as little organization of cytoplasm about it as can be found in any angiosperm. Thus there has been a gradual reduction of the archegonium from a condition almost like that of the pteridophytes to the most extreme condition found in angiosperms.

Some might suggest that such reductions would have their natural termination in the elimination of all sexuality, with apogamy as the goal. In *Gnetum Ule* there seem to be instances of apogamy. In the cases reported as apogamy in *Pinus* there is the possibility of fertilization by the ventral canal nucleus. Personally, I prefer to regard apogamy as a specialized, unnatural phenomenon, and not as a condition toward which plants are moving.

The behavior of the chromatin in the final stages of both spermatogenesis and oogenesis in gymnosperms seems to be unique. At the formation of the ventral canal cell or ventral canal nucleus, the chromosomes are very small. The ventral nucleus or cell soon disintegrates, but the chromosomes of the egg nucleus form a spirem. From this point there is a period of develop-

ment for which we have no satisfactory account of the chromatin. The coarse reticulum of the egg nucleus is not chromatin, for most of it may remain after chromatin again becomes demonstrable. To say that the chromatin becomes dissolved in the linin or takes the form of coarse granules or nucleoli, which may or may not be chromatin at all, hardly solves the difficulty. That some of the so-called metaplasm has about the same position as the latest recognizable stages of the spirem, seems to be about all that can be said. It is certain that chromatin has not yet been traced from the telophase of the ventral canal cell mitosis to the resting egg nucleus with any such certainty as in the pteridophytes and angiosperms. The organization of the spirem from the dubious contents of this nucleus has not been traced in any satisfactory way. However, it is perfectly certain that a small and beautifully definite spirem finally appears.

Fertilization

To the cytologist, who is likely to attribute extreme importance to chromatin, these reduction series in the formation of eggs and sperms are very important, since the more there is eliminated from the structures taking part in fertilization, the more accurately can we determine what is essential and what only accessory.

Fertilization has been studied more thoroughly in *Pinus* than in any other gymnosperm. Here each archegonium has its own archegonial chamber and the pollen tube entering it necessarily discharges its contents into the one egg, the two male nuclei, together with the stalk and tube nuclei and also more or less cytoplasm and starch all entering the egg. One of the male nuclei comes into contact with the egg nucleus and the nuclear membranes at the point of contact break down, so that the chromatin of the two nuclei becomes surrounded by the membrane of the egg nucleus. A spirem is formed from the chromatin network of each of the sex nuclei and each spirem segments into 12 chromosomes, so that there are twenty-four chromosomes. These do not fuse with one

another, but become so mixed that the male and female chromosomes can not be distinguished. Each chromosome then splits and during the completion of the mitosis twenty-four chromosomes go to each pole to form the first two nuclei of the sporophyte generation. Consequently, during this process which we call fertilization, there has been no blending of the chromatin contributed by the two parents. Whether a real blending takes place as the two groups of chromosomes pass from the telophase of the first mitosis into the resting reticula of the daughter nuclei, is still undetermined. Personally, I am inclined to think that there is no blending, either at this early stage or later, but rather, that the chromatin contributions remain distinct throughout the life history. Whether there is, during the synapsis stage of the reduction division, sufficient fusion to impair the identity of the individual chromosomes, still remains to be demonstrated.

Although the chromosomes of the two groups become so mixed that they can not be distinguished, the well-known mechanism of mitosis makes it certain that one half of each chromosome contributed by the two parents will reach each of the two daughter nuclei resulting from the first division of the fertilized egg. The same mechanism of mitosis makes it very probable that this equal representation of the two parents will continue throughout the life history of the plant.

In all the genera which have been studied, more or less cytoplasm enters the egg with the male nucleus. In the cycads the entire sperm enters the egg and the cilia may continue to move after the sperm is within the cytoplasm of the egg, but the nucleus of the sperm soon slips out from the cytoplasmic sheath and advances toward the egg nucleus, leaving most or all of the cytoplasm in the upper part of the egg. In other forms, like *Torreya, Juniperus* and *Taxodium* the cytoplasm of the male cell surrounds the fusion nucleus and takes part in the formation of the embryo, but in most genera, no such cyto-

plasm is visible and the embryo is formed from a rather small portion of the basal region of the egg, quite remote from whatever cytoplasm may have entered the egg with the male nucleus.

On such evidence we could not claim, logically, that cytoplasm does not play an essential part in inheritance, for the egg at its first segmentation contains cytoplasm brought in with the male nucleus, but we believe that the series which we traced in spermatogenesis presages the final elimination of any cytoplasm as a part of the male contribution, and the series could be carried into the angiosperms, where, in some cases, the male contributes only a nucleus without any cytoplasm.

In nearly all the gymnosperms the immediate response to the stimulus of fertilization is a series of nuclear divisions which follow each other in such rapid succession that no cell walls are formed between the nuclei. The divisions are simultaneous, probably because the nuclei are in a common mass of cytoplasm exposed to the same conditions. In the large eggs of the cycads, the free nuclear divisions continue until there may be more than a thousand nuclei, but in forms with smaller eggs, the period of free nuclear division is correspondingly reduced, so that we can select a series of genera which show more than a thousand free nuclei, 256 nuclei, then 32, 16, 8, 4 and finally no free nuclear division at all, the first nuclear division of the fertilized egg being followed by the formation of a wall between the daughter nuclei.

These early stages in the gymnosperm sporophyte are remarkably like the early stages of the gametophyte, which also has a prolonged period of free nuclear division before walls begin to be formed, but the conditions are also very similar. The most striking difference between the sporophyte and gametophyte in these early stages is that during mitosis one shows twice as many chromosomes as the other. Very soon, of course, the two generations become very dissimilar. It is worth recalling, in this connection, that in some algæ, like

Dictyota and *Polysiphonia*, the two generations remain similar throughout the vegetative period, the only distinguishing feature being the number of chromosomes.

In conclusion, we believe that fertilization is a phenomenon of fundamental importance, and that future investigation dealing especially with the differences between the various chromosomes, differences which may be only fortuitous but which may be constant and important, may throw light upon the problems of variation and heredity. That the fusion of gametes always gives rise to a sporophytic generation and necessitates a reduction of chromosomes somewhere in the life history is not so speculative and the claim is readily admitted for plants above the thallophytes. We believe that it holds even for thallophytes.

In the simplest bryophytes, alternation is already too thoroughly established to throw any light upon the origin of the phenomenon, and the same may well be said of algæ like *Dictyota, Cutleria* and *Polysiphonia.* We believe that even where the first division of the zygote or fertilized egg shows the reduction division, as in *Coleochæte,* there is a true alternation of generations, although the sporophyte generation is very short. The test of a sporophyte is not its longevity. The fertilized egg of a lily is the first cell of the sporophyte, whether it ever divides at all. Consequently, we regard the zygospore of *Ulothrix* or *Spirogyra* and the fertilized egg of *Vaucheria* or *Œdogonium* as sporophytic structures, even if the first division of the zygote should be meiotic, as seems probable. From such a simple beginning, we believe that the more complex sporophytes with more conspicuous alternation have been developed. The gymnosperms throw no light upon the origin of alternation, but show suggestive stages in the reduction of the gametophytes. They also afford an admirable field for the study of some aspects of fertilization, but we can hardly claim that all the problems of this complex phenomenon would be solved with greatest certainty by the study of cycads or pines.

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN ANGIOSPERMS[1]

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WHAT constitutes sexual reproduction, fertilization or fecundation is so variously set forth in botanical literature that one naturally approaches a discussion of this subject with some timidity. Having been assigned the group angiosperms, in which a definition of sexual phenomena may be made more specific by concrete illustration, it seemed at the outset that a part of my task, at least, was simpler than that of some of my colleagues who take part in this section of our program; but a moment's thought convinced me that what might be gained from this limitation of my field was probably much less than the opportunities offered by the scope and diversity of phenomena in groups of lower plants.

In the preparation of this paper, the writer has kept clearly in mind the fact that the phenomena of sexual reproduction implies explicitly that a special significance is attached to the nucleus as in a large measure distinct from any function, or rôle of the cytoplasm; consequently he will deal first chiefly with nuclear behavior, leaving a discussion of the relation of nucleus and cytoplasm to be dealt with in a later paragraph.

Sexual reproduction in phanerogams implies the union of especially developed cells known as gametes, and the development of an individual plant from such union. While in this process the union of the nuclei is held to be more important, it is not inferred that the part taken by the cytoplasm is unimportant, but the writer does insist that the cytoplasm plays a secondary rôle in the

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most important results of sexual reproduction, namely, the transmission of parental characters. It will be maintained also that the union of mere gametophytic cells does not constitute fecundation, or a sexual process in phanerogams, nor is parthenogenesis—if such really exists in seed plants—to be confused with apogamy, nor apogamy with the various sorts of vegetative propagation of the sporophyte. Lastly, it is likewise the duty of the student of fecundation to consider the phenomena of graft hybrids which have been reported in recent literature, for such phenomena may have a profound significance in the shaping of future theories of sex and heredity, and on sex determination and control.

The problem of sexual reproduction in higher plants, and in lower ones as well, is complicated by the existence of two distinct phases, or individuals, in a life cycle, namely, the gametophyte and sporophyte; for it is necessary, in dealing with the rôle of the nucleus in sex, to consider a complete life cycle. Now gametophyte and sporophyte in phanerogams are fundamentally different hereditarily, and this difference is due chiefly to the fact that the former possess the haploid, or x number, of chromosomes, and the latter the diploid, or $2x$ number. Whatever respect or disrespect one may have for the "sacred" x and $2x$ number of chromosomes, the fact of their importance in any theory of sex and heredity remains the same, and must be taken into consideration. It is, of course, quite familiar to all that the change from sporophyte to gametophyte occurs in the formation of the spores, and that this change consists in the reduction of the number of chromosomes from the diploid, $2x$, to the haploid, x number; that this reduction is accomplished during the first mitosis in the spore mother-cells, this division of the nucleus being acknowledged as qualitative or differential. A detailed description of the evolution and behavior of the chromosomes during the tetrad divisions, and a discussion of controversies and of the different views held in regard to this evolution, or in regard to the differential character of any chromo-

some or set of chromosomes—are features which can not find consideration within the limits of this paper. I wish to state also that in the use of the expression, sexual reproduction, I shall keep in mind primarily, and for the sake of clearness, what will be called a complete sexual angiosperm, hereditarily speaking, that is, one with a complete life-cycle, embracing both sporophyte and gametophyte. Such an individual arises from the fusion of egg and sperm, each with the haploid number of chromosomes. The product of this fusion must develop into an adult sporophyte, capable of producing functional micro- and mega-spores, each with the haploid number of chromosomes. From this it will be seen that the mere fusion of gametophytic cells or nuclei is not necessarily regarded as a sexual process. It is to be understood also that the writer does not consider it imperative to stay within the confines of the foregoing definition, for like nearly all general definitions, this is made for convenience and for greater clearness in the general presentation.

No profounder statement has been made within the past half century than when it was said that the union of two sexual cells created a new individual—the individual with just twice the number of chromosomes as that possessed by either parent cell, namely, a sporophyte; for is it not the sexual process that makes possible all those phenomena understood by the expression, transmission of parental characters to offspring? And I mean especially the transmission of characters of two direct parents to each new generation. In this connection may we not ask also whether hereditary phenomena, such as engage the attention of biologists at the present day, exist among those simple plants in which sexual reproduction does not occur? Is there such a thing as phylogeny in plants that are without sex? The limits of this paper prohibit an attempt at an answer to the last two questions at this time. We shall have in mind then those characteristics which are handed down from parents to offspring. Some of these characters may mani-

fest themselves in the progeny with varying degrees of intensity, or in such combinations that entirely new marks or characters may appear; consequently characters are spoken of as dominant, recessive, latent, etc., and it not infrequently happens that estimates are placed upon absent characters. All of this implies that these external marks of living things are the manifestations of the activities of certain parts of the living substance, which are in competition, or among which there is an unceasing struggle. Attempts are also made to predict, by means of mathematical formulæ—and with surprising success in some cases—which of these forces or activities will gain the upper hand and dominate, and which will be secondary. Furthermore, sexual reproduction in phanerogams always implies a something that we know as maleness and femaleness, and this maleness and femaleness are phenomena which distinctively characterize the gametophytes. Maleness and femaleness may, in certain cases, give a distinctive mark to the sporophyte, as in diœcious plants, if we admit that such a thing as an absolutely diœcious sporophyte exists in angiosperms. But male and female marks are first manifested in the sporophyte of most seed plants by the production of the pollen and of the megaspores, which production is, of course, a matter of heredity. In the formation of pollen, it is well known that it is the nucleus which undergoes the important and complicated changes in division; the cytoplasm, so far as present knowledge extends, is halved arbitrarily. The same is likewise true in the development of the megaspores. In the case of each spore mother-cell, a qualitative division takes place, by which, as experimental evidence seems to indicate, different intensities of maleness and femaleness pass respectively to the several resulting cells. Both male and female gametophytes with their developing gametes grow under similar environmental conditions, namely, that of a parasitic habit within living tissue. The sperms of the pollen tube consist mainly of nuclei, with scarcely any distinctive characteristics in the[illegible]ty

cytoplasm. These nuclei contain the haploid number of chromosomes. In the development of the egg, the same number of chromosomes is strictly preserved, no matter what mitotic peculiarities may be observed in any other cells of the embryo-sac, apart from the egg-apparatus. The egg differs from the sperm in appearance chiefly in the amount of cytoplasm present, but the cytoplasm of the one is similar to that of the other. Apart from difference in shape, which is of no importance in phanerogams, the sexual nuclei reveal identical chromatin structures at the time of union, for both are in the resting, or non-mitotic state. Chromatin granules of the sperm nucleus mingle with those of the egg. When the nuclear membranes between the two contiguous nuclei have disappeared, it is not possible to distinguish paternal from maternal chromatin. It is not seen that chromatin particles of the sperm fuse or become paired with those of the egg nucleus. The gamete nuclei do not remain in any manner separate or distinguishable from each other, as in certain lower plants and in some animals, and one of the very interesting and important problems from the standpoint of hereditary considerations is the relation of male and female chromatin, during the life of the sporophyte. A number of authors have offered explanations of this relation based on observations made upon the first, or heterotypic, mitosis in the spore mother-cells, *i. e.,* at the end of the sporophytic cycle. Strasburger ('05) and Gregoire ('05), together with a number of their more recent students, maintain that the maternal and paternal homologous chromatin parts become associated in pairs previous to and during the synaptic balling up of the nuclear contents in the first mitosis of the spore mother-cells. This process, they assert, leads to the formation of two spirems (one paternal and one maternal) which become united side by side, to form the double chromatin thread, in which the homologous parental chromatin parts are brought near to each other.

The writer (Mottier, '07, '09) does not agree with this

view. From a careful and extended study of mitosis in spore mother-cells of higher plants, he is convinced that, confirming the observations of Farmer ('05) and others, there is no development of maternal and paternal spirems which unite laterally to form the double chromatin thread or spirem in the mitosis under consideration, but that the sporophytic chromosomes are arranged in a lineal series in the heterotypic spirem, and that consequently the two members of each bivalent chromosome are brought side by side, in case such an arrangement is attained by the two members of each bivalent, by a folding, looping or lateral approximation of parts of the spirem. In his own studies the writer is unable to find any justification of the doctrine that maternal and paternal chromatin is represented in definitely recognizable lumps designated by some observers as prochromosomes. While I can not agree with the view advocated by Strasburger and Gregoire, namely, the presynaptic or synaptic union of two spirems (male and female), because of my personal studies, I am also unable to accept their explanation upon the ground of theoretical considerations. Let us return for a moment to the fusion nucleus of the fecundated egg. It is perfectly clear that, soon after nuclear fusion, paternal chromatin elements, let us say, pangens, are indistinguishable from maternal elements. These pangens, assuming always the individuality of the chromosomes and of the pangens, correspond in form, size and staining qualities. The nucleolus or nucleoli of the egg are also similar to those brought in by the sperm, in case nucleoli are demonstrable in the sperm nucleus. There is nothing to lead one to believe that the parental pangens do not mingle in the resting nucleus (*i. e.,* not in mitotic activity). If there is a pairing of homologous parts, or exchange, inter-relation, or "Wechselwirkung" of pangens, or of any hereditary bearers, what reason is there to believe that such should not take place soon after fecundation, rather than at the close of the sporophytic ontogeny, or the beginning of gametophytic develop-

ment? If the nature and development of the sporophyte, from the standpoint of its inherited characteristics, is determined by what is transmitted to it by its parents, how may these parental tendencies operate unless they are intimately associated—unless some mutual relation, or a "Wechselwirkung" of the entities representing these tendencies, is in continuous activity? Furthermore, when the fusion nucleus of the fertilized egg in angiosperms divides, the spirem separates by cross segmentation into the $2x$ number of chromosomes, x being male and x female. These sporophytic chromosomes are arranged in lineal series, or end to end, to make the spirem, which splits longitudinally. I do not believe many cytologists will contend that the sporophytic spirem is formed by the lateral coming together of male and female spirems. If the parental chromosomes are arranged tandem to form the sporophytic spirem, why should they be arranged in any other manner to form the heterotypic spirem?

Returning now to the fecundated egg, it is seen that the fusion nucleus presents the same visible structure as that of either gamete, with the exception that an additional nucleolus or nucleoli may sometimes be observed. The essential demonstrable act in this fusion concerns the nuclei; the behavior of the cytoplasm that may accompany the sperm nucleus is largely a matter of conjecture, for it is not possible to trace its behavior with any degree of accuracy, either in the living state, or by means of the indirect method of study. However, to satisfy the demands of the most radical we may admit that sperm cytoplasm unites with egg cytoplasm in the act of fecundation. I have described in some detail the structural union of the sexual nuclei; for in a later paragraph will be discussed the relative significance of nucleus and cytoplasm in sexual reproduction, and as factors in the transmission of hereditary characters.

One male nucleus of the pollen-tube is concerned in sexual reproduction as that term is understood in this paper, but as the union of the second male nucleus with

the polar nuclei in a number of plants has been associated with, if not actually regarded as, a sexual act, the phenomenon will receive a brief mention. In 1897, the writer (Mottier, '97) called attention for the first time to the fact that the second male nucleus applied itself to one of the polar nuclei in *Lilium Martagon,* and shortly after that date the actual union of this male nucleus with the endosperm nucleus of the embryosac was reported for various plants by different observers. Guignard spoke of this nuclear union as a second fecundation, hence arose the idea of "double fecundation" in phanerogams. The fusion of the two polar nuclei and the second male nucleus resembles physically the real sexual union, as do also nuclear fusions in ordinary vegetative cells wherever such may occur. It recalls a sexual act in subsequent behavior, for it is maintained that endosperm thus arising is of a hybrid character, and that this hybrid character is due to the hereditary influence of the male nucleus. The hereditary influence of the second male nucleus upon the endosperm we may admit for the sake of argument, for whatever else this phenomenon may signify, it certainly shows the greater importance of the nucleus in the transmission of characters. But, that this union of nuclei in the endosperm cell is not a sexual process, as defined in a foregoing paragraph, is seen in the fact that the endosperm is merely a continuation of the female gametophyte, developed subsequent to fertilization of the egg, and for the nourishment of the sporophyte, just as a fern prothallium may continue its development, following the fecundation of an egg and its subsequent development into the embryo fern.

In a group of organisms in which a structure or function is so universally present, the absence of the same in any one or several of such organisms elicits at once our attention, and, in this respect, apogamy and parthenogenesis become of special interest. Although apogamy and parthenogenesis do not involve the sexual act, yet an accurate and intimate knowledge of these

phenomena is likely to modify profoundly our views of sexual reproduction, especially if a series of generations of apogamously produced plants be compared with a series of sexually produced individuals, of the same or related species, in regard to the subject of variation, individual vigor, manner of propagation, transmission of certain characters, etc. The term apogamy is here used to signify the development into an embryo of the egg-cell possessing the double or $2x$ number of chromosomes without the union with a sperm nucleus from the pollen-tube (somatic parthenogenesis of Winkler, parthenopogamy of Farmer and Digby). It is not deemed desirable to connect the word parthenogenesis with such a process, for a reproductive cell, although developed morphologically as a gamete, is not so considered unless it contain the reduced number of chromosomes. Accordingly, the term parthenogenesis will be applied only to the development into an embryo sporophyte of an egg containing the x number of chromosomes.

In recent years several notable cases of apogamy among phanerogams have been described, among which may be mentioned *Antennaria alpina* by Juel (1900), species of *Alchimilla,* especially of the group Eualchimilla by Murbeck and Strasburger ('04), *Taraxacum officinale* by Juel, *Wikstroemia,* by Winkler, together with several others from different families of plants. In *Antennaria alpina,* for example, the tetrad divisions do not take place in the megaspore mother-cell which functions at once as the megaspore. Naturally this cell contains the diploid number of chromosomes. From this cell there develops an apparently normal embryo sac, with the exception that the polar nuclei do not unite. The cell which represents the egg develops without fecundation into an embryo sporophyte. The process in the other species mentioned is in the main similar to that of *Antennaria alpina,* differing only in certain details, which may not be enumerated here. While, in these apogomous species, an apparently normal gametophyte develops, it may be very seriously questioned

whether such embryosacs, whose egg-cells contain the these apogamous species, an apparently normal gametophytic. However, progress in science is not accomplished by controversies and discussions of terminology. The main thing which interests us here is the effect, from an hereditary standpoint, that apogamy, of the sort mentioned, has upon the species so affected. True it is that such apogamous progeny have the characters of both parents, male and female, but it is a remote parentage. There is no new parent introduced with each new generation, that is, each time a plant comes from a seed, and it seems not improbable that the loss of certain very important reproductive functions may be expected in later generations of such plants. In reality certain observed facts seem to bear out this suggestion, as Strasburger found that, in some of the Eualchimillas, degeneration took place in the pollen mother-cells before the spores were fully formed. Whether apogamously developed plants will behave in a manner similar to those propagated vegetatively, *e. g.*, by cuttings, or as normal sexually produced individuals, future research must determine. Until the observations of the several observers have been confirmed by others, and until experimental cultural studies are made to ascertain the behavior of apogamous plants along with those possessing sexuality, speculation seems idle.

In regard to parthenogenesis as defined in a preceding paragraph, this phenomenon is claimed to occur in certain species among rather widely separated families. The best known instances are *Thalictrum Fendleri,* as reported by Day (1896), *Thalictrum purpurescens,* by Overton (1902, 1904) and *Wikstrœmia indica,* by Winkler (1904, 1905). However, for *Thalictrum purpurescens,* Overton (1904, p. 278) expressly states that in some cases no reduction in the number of chromosomes occurs in the embryosac mother-cells, and that tetrads are not formed, so that apogamy certainly occurs in this species also. In regard to *Wikstrœmia* it may be added that the recent investigations of Strasburger upon this

plant and other Thymelaceæ, point rather towards apogamy than parthenogenesis.

Even more perplexing to the student of sex and heredity than apogamy or parthenogenesis are the phenomena presented by what are known as graft hybrids. A number of seed plants of a hybrid nature are known to botanical science, which have not arisen by means of seed production, but presumably from the callus formed at the juncture of the stock and scion in grafting. The most noted of these is, of course, *Cytisus Adami,* which is supposed to have arisen from *Cytisus laburnum* and *Cytisus purpureus* as a graft hybrid. This problem, which has held, in a large measure, the interest of biologists for about eighty years, seems now to be on a fair way towards a solution, having as a starting point the production of a graft hybrid experimentally. Hans Winkler, as is well known, has produced a plant which, in point of flower, fruit and foliage, seems to be a hybrid between the common nightshade *Solanum nigrum* L. and the tomato, *Solanum lycopersicum* L. of the King Humbert yellow-fruited variety, by an ingenious method of grafting in which the nightshade was used as the stock and the tomato as the scion. Perhaps a very brief statement of the process may not be out of place here.

Using the cleft method of union, Winkler grafted vigorous shoots of the seedling tomato upon the stem of the nightshade. As soon as union had taken place the scion was cut off near its base in such a way that the apical cut surface consisted partly of nightshade and of tomato tissue. Of the adventive shoots arising only those which sprang from along the line of union of the two specifically different tissues were allowed to grow. In one particular case fourteen of such sprouts were removed and transplanted as cuttings. Of these eight proved to be *Solanum nigrum,* five pure *Solanum lycopersicum,* and one the hybrid in question. This plant grew to flower and fruition, and as stated in the foregoing, revealed hybrid characters in stem, leaf, flower and fruit. This hybrid Winkler named *Solanum*

tubingense H. Wklr. (*S. nigrum* L. + *S. lycopersicum* L., 1908). For a detailed description of the plant the reader is referred to the original publication.[1] That the conditions under which such a graft hybrid is produced are very rarely fulfilled, is seen in the fact that from the 268 graftings made by Winkler in 1908, 3,000 adventitious shoots were developed after decapitating the graft in the manner described, and of these 3,000 the vast majority were specifically pure; five were chimeras, and one the hybrid referred to. Now the all-absorbing question for the cytologist is: By what means are parental characters transmitted in cases of this sort? Of course speculation is futile until the histological facts are known, but, assuming that such shoots are real hybrids, two guesses may be offered. There may have been (1) a migration of nuclei from cell to cell and their subsequent fusion, as in certain fern prothallia developing apogamous sporophytes, or (2) the hereditary transmission may have been accomplished by cytoplasmic union between cells, or by some sort of enzyme action.

It is highly probable that these remarkable adventitious shoots are not true hybrids, but mere chimeras.

In a personal communication, Dr. Winkler has very kindly informed me that seeds of "*Solanum tubingense*" produced pure nightshades (*Solanum nigrum*), and those of "*Solanum proteus*" pure tomatoes (*Solanum lycopersicum*).

The fact that seeds of "*Solanum tubingense*" produced pure nightshades seems to be conclusive evidence that the structure in question is not a hybrid, but merely a remarkable chimera. Strasburger ('09) has just published the results of a histological study of the tissues formed at the juncture of stock and scion in grafts of *Solanum nigrum* and *Solanum lycopersicum*, and he reports that neither nuclear migrations from one vegetative cell to the other nor nuclear fusions in any of these cells were observed. These results are in accord with the same author's cytological studies on other supposed

[1] *Ber. d. Deutsch. Bot. Gesellsch.*, 26*a*: 595–608, 1908.

graft-hybrids. Winkler's histological studies on "*Solanum tubingense*" have not yet been made public, but all the facts thus far seem to indicate that so-called graft-hybrids, including *Laburnum Adami,* the *Bizzarrias* and those of *Mespilus,* etc., are only vegetable chimeras.

At the juncture of stock and scion in grafts, especially in the case of those that produce adventitious shoots of such remarkable character, there is a cell-complex formed of the vegetative cells of two specific individuals, and the specifically different cells may be regarded as being so intermingled and reacting upon each other in such a manner as to produce adventitious shoots of an almost exact hybrid character in so far as vegetative marks are concerned. In the case of Winkler's "*Solanum tubingense,*" whose seeds gave only pure nightshades, it is clear that both egg and pollen were descended from pure nightshade cells, as the nightshade and the tomato do not cross.

Although the problem of the so-called graft hybrids can not be regarded as definitely settled, yet nearly all the facts go to strengthen the view that hybrids are formed only by the union of cells and nuclei sexually differentiated, and that fecundation and the transmission of characters are not accomplished by the protoplasm in general, nor by the action of an enzyme, nor is it the expression of metabolism, but by the *union of specific material entities in the sexual nuclei.*

Although the concensus of opinion among biologists attributes to the nucleus by far the most important rôle in the process of sexual reproduction in its fullest significance, yet there is still some difference of opinion in regard to the relative functions of nucleus and cytoplasm in imparting the stimulus to growth and cell division, and in the transmission of parental characters—the two chief constellations of phenomena following the sexual act.

To arrive at any satisfactory conclusion in the light of existing literature, a careful analysis of cell structure and of the functions more directly concerned is neces-

sary, both from the standpoint of phylogeny and from that of the individual, or individuals concerned. Careful investigations of recent years upon the cells of certain lower plants seem to justify the opinion that the more original or primary protoplasm is to be conceived as being entirely without organized nuclei, possessing uniformly in all parts its formative and nutritive functions. Then there gradually came about, phylogenetically speaking, a separation of the constructive, nutritive—and may we also say—directive functions in this substratum, those parts of the plasm having formative activities being the first differentiated bearers of hereditary characteristics. These particles or granules may have remained for a long time distributed in the general plasmic mass, just as we find in certain existing Cyanophyceæ and bacteria "chromatin bodies" distributed throughout the cell rather than collected in a typical nucleus. The next step in the evolution of more differentiated protoplasm occurred when the formative parts, be they known as chromatin bodies, or what not, became separated from the surrounding plasm by a membrane, or, in other words, the creation of nucleus as distinct from cytoplasm. In the light of known facts no one, I think, will seriously believe that among the lower plants the nucleus is as highly differentiated as among seed plants, consequently a larger number of functions must have been performed by the various hereditary units, and a much simpler method of nuclear division demanded. This view seems well borne out by the simpler method of nuclear division in certain lower plants and in cells of higher plants, which have taken on a purely vegetative rôle, and which divide by the direct method or fragmentation. As soon, however, as differentiation in the hereditary units increased, a much greater complexity in the mechanism of division followed, a conclusion to which the mitotic phenomena in higher plants stand as incontestible testimony. On the other hand, we do not mean to imply that progressive differentiation was confined to the nucleus alone, for the cytoplasm of higher plants reveals

evidence of unmistakable differentiation. I do not allude to the alleged hereditary substance, chondrosomes, to be mentioned beyond, but merely to such differentiation as spindle fibers, which in many higher plants are almost wholly of cytoplasmic origin. As is well known, Strasburger has endeavored to make things clearer by applying to such parts of the cytoplasm as spindle fibers centrosomes, centrospheres and the plasma membrane of the cell, the term kinoplasm, attributing to this substance certain activities. The researches of Noll upon marine algæ indicate with a very high degree of probability that the plasma membrane is the part of the protoplasm which takes a leading part in responding to external stimuli. The doctrine that an enucleated cell can not do any constructive work, as, for example, forming a cellulose wall, has become so generally accepted that the same has found its way into general reference works. This doctrine has in recent years been disputed, but so far as I am aware it has not been satisfactorily disproved. I shall not bring into this category such cytoplasmic differentiations as chloroplasts and other plastids, but enough has been said to indicate that the cytoplasm as well as the nucleus is a differentiated body, which means a diversity of functions or activities. Now, although cytoplasm and nucleus have certain functions that seem in a large measure independent, yet the interrelation of these two parts of the cell is such that neither can exist and function to any great extent without the other. No one has up to the present time been able to isolate a nucleus and keep it alive any length of time apart from living cytoplasm. Whatever the nucleus does, it must do in connection with living cytoplasm. The cytoplasm is in a sense the special environment of the nucleus, and it is in this environment that the nucleus must exist and function. It is also reasonable to believe that, in certain functions of the nucleus, the cytoplasm acts largely as an environmental factor. It is, however, an environment so intimately connected with the nucleus that even a momentary separation may prove fatal, for the skill of

the experimenter in this field is yet to be demonstrated.

On the other hand, while the cytoplasm may exist for some time wholly apart from a nucleus, and although during this separate existence the cytoplasm may respond to certain stimuli, yet it can not do constructive work—a phenomenon which seems to indicate roughly the chief province of these two parts of the living cell.

In the light of the foregoing analysis, we may now consider some results obtained by indirect methods, and through certain experiments.

Since the declaration of O. Hertwig in 1875, that fecundation consisted essentially in the union of an egg and a sperm nucleus, this doctrine has received general acceptance. Some observers maintain that this idea places undue emphasis upon the importance of the nucleus, and claim that the cytoplasm is almost of equal significance. In a recent publication Meves ('08) describes in great detail rod or thread-like bodies in the cells of the very young embryo of the chick, which he designates as chondriosomes, and which he regards as cytoplasmic bearers of hereditary characters. The same author in 1904 described and figured similar rods and threads as occurring abundantly in the tapetal cells of *Nymphæa alba*. In the tapetal cells of the anther of *Ribes Gordonianum,* Tischler ('06, p. 573) calls attention to slender rods of varying length, which he designates as chromidial substance, stating that they came out of the nucleus. The writer has examined many thousands of tapetal cells from various plants, fixed and stained in a manner quite similar to that used by Meves, but no such bodies have been found as those figured by this author. It is not my intention to discuss this phase of the subject from the standpoint of zoological literature, but it may be said that tapetal tissue is not the place that a botanist would go to look for especially differentiated hereditary substance. If hereditary substance, such as Meves attributes to the cytoplasm of tapetal cells, really exists, it seems very strange to a plant cytologist that it can not be demonstrated in spore mother-cells, where,

above all parts of the plant, protoplasmic structures are most clearly brought out.

As stated in the foregoing, fecundation manifests two constellations of phenomena, the transmission of parental characters and the power of growth and division of the egg. That these two categories are in a measure distinct is amply attested by phenomena of common observation, and by experimental evidence. That various sorts of environmental stimuli, from the sting of an insect to the increased osmotic power of surrounding water, will impart to living cells the power of growth and division is well known. The sting of an insect, for example, will stimulate growth and cell division in stem and leaf, which results in a gall; the presence of a pollen tube will induce an ovule to grow to mature size though no embryo develops within it. In these and in other similar cases, too numerous to mention, we have merely responses to external stimuli, for doubtless the pollen tube may act as an external stimulus, and no one will contend that these phenomena have to do with the transmission of parental characters. From our standpoint the phenomenon of artificial parthenogenesis merits especial attention. When the egg-cells of certain marine animals are stimulated to develop by external agencies of whatever sort, it has become fashionable to speak of the fact as fertilization, but whatever meaning be put into the word fertilization, the phenomenon in question is not fecundation or sexual reproduction. Even though in every case the most sanguine expectations of the experimenter be realized, namely, the development into an adult of an egg thus stimulated, the process would teach us nothing more about sexual reproduction and the transmission of parental characters than ordinary parthenogenesis. The fact that a larva having purely maternal characters will develop from a sea-urchin egg with which the sperm of a starfish had united, does not show that hereditary characters are handed down by the cytoplasm. If, on the contrary, the gastrula, showing only maternal characters, which Godlewski ('06) reared

from the union of an enucleated egg-fragment of the sea-urchin and the sperm of a crinoid, could have developed into an adult, or even into the larval stage, which still revealed only maternal characters, the cytoplasm might have regained some of its old-time prestige, but even then it is doubtful whether that fact would have wrested from the nucleus its monopoly as a transmitter of parental characters.

In such cases as the embryo hybrid of sea-urchin and starfish, mentioned in the foregoing paragraph, it seems very probable indeed that the cytoplasm of the egg directs and even controls the growth of the embryo for a short time subsequent to fecundation, but it is very improbable that the cytoplasm does more. Even in the case of a complete fusion of the egg and sperm nuclei, this and similar experiments seem to indicate only the dominance of the egg nucleus over that of the strange sperm. With the egg nucleus operating in its own special environment, and attributing a directive or regulative function to the cytoplasm, the result is what might reasonably be expected. That the cytoplasm is differentiated, and that it directs or regulates the formation of certain parts of the embryo in some animals, is clearly shown by the various interesting and important studies of cell lineage carried out by Conklin ('05) and others. Important and far-reaching as are these studies in contributing to our knowledge of living protoplasm, they do not teach us very much concerning the cytoplasm as an heredity bearer, nor do I understand that the respective observers make such claims.

The stimulation of egg-cells to growth and division by immersing them in water having different physical or chemical properties than their normal surroundings, or by injecting chemicals into the ovaries or ovules by means of an hypodermic syringe, are lines of study that are valuable and interesting in showing the response of living cells and tissues to external stimuli, for it is the business of the physiologist to know what cells can do under any and all conditions; but that these experiments

have anything to do with sexual reproduction or in elucidating the more fundamental principles in the evolution of organisms connected with sexual reproduction, still remains to be seen.

On the other hand, if one regards the elementary life processes merely as the expression of metabolism, then hereditary peculiarities are only the expression of metabolism. That which is inherited is for each organism only that kind of metabolism peculiar to the organism. Of course, the writer can not subscribe to this view. Neither does he maintain that the cytoplasm takes no important part in sexual reproduction. He has called attention to the opinion that the stimulus to growth and cell division which follows every sexual act fully accomplished, and which may be brought about apart from the act of fecundation, has been confused with the main result of sexual reproduction, namely, the transmission of parental characters. It is held that the present state of our knowledge still maintains the doctrine that the "monopoly" of transmitting hereditary characters still belongs to the nucleus, and that these hereditary parental characters are represented in the nucleus by material entities. It matters little whether we speak of these material representatives as pangens, or what not. The opinion is expressed that the chief function of the cytoplasm, apart from purely nutritive activities, in its relation to the nucleus is directive or regulative in the sense of being responsive to external stimuli. In so far as the transmission of parental characters go, the cytoplasm plays about the same rôle compared with the nucleus as the environment does in the development of the individual organism.

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SHORTER ARTICLES AND DISCUSSION

STERILITY[1]

THE problem of sterility presents many points of interest to the biologist, whether he be a clinician, breeder of plants or animals or a pure biologist, both from a descriptive and an experimental aspect. By the physician, the failure of individuals to produce children in marriage is designated by this name, although the causes may be widely at variance in different cases. Thus, the failure may be due to the impotence of the male, induced by a variety of causes, such as congenital impotence, where sex cells are not formed, although the organs themselves may be apparently normal; or evident deformities may occur such as the failure of one or both testes to descend (cryptorchism); again, impotence may be induced by disease, such as gonorrhœa, syphilis and the like; or again, through presenile debility caused by excessive activity of the organs concerned. On the other hand, the failure to produce offspring may be due to the corresponding impotence of the female, or it may result from wholly secondary causes, such as the failure of the ovum to become fixed. All of these cases are grouped, collectively, under the term sterility. Very frequently a simple operation upon the uterus of the female is sufficient to cause the ovum to become fixed, so that subsequent ovulations, accompanied by fertilization, result in offspring and the sterility disappears. With congenital sterility, where no sex cells are formed, the case is obviously different, for the condition there is permanent. Cases of congenital sterility seem to be rare, although it is exceedingly difficult to obtain concise data upon the subject. The impotence caused by disease may, in time, disappear, especially if the ravages of the disease have not destroyed the germ cells, as is often the case. An impotence ascribed to psychical causes may rarely occur, but concerning this factor, we have, obviously, little or no exact evidence.

The sterility induced in crossing animals and plants belonging to different varieties and species has long been known. The

[1] Presented at the fourth evening seminar of the Harpswell Laboratory, August 2, 1910.

early hybridists of plants, Gärtner, Kölreuter, Nägeli, Gordon and others, were familiar with the frequent failure of pollen, placed upon the stigma of certain plants, to produce seed in the ovules of that plant, and with the fact that even if seed is obtained, it may not grow when planted. Kölreuter and Gärtner saw in sterility the criterion whereby species may be distinguished. If two forms bred together produced seed, and the seed was capable of growing into perfect plants, the two forms were considered as belonging to the same species. If, on the other hand, no seed was produced, or if produced, this seed was incapable of growth, the two forms were considered as belonging to distinct species. However, as Darwin points out, these two workers were biased in their appreciation of sterility, as a valid criterion for distinguishing species, for they themselves, as have indeed all workers since them, described all degrees of sterility under such circumstances, from slight deviations in form of the hybrid plants, through a condition where the seed, although formed, was shrivelled and incapable of producing the young plant, to complete sterility, where no indication of even a pollen-tube is seen in the style of the pistil. Obviously, the personal equation of the experimenter will be a potent factor in determining whether there were two species, or a single one involved in questionable cases, and the definiteness of the criterion is largely detracted. To Darwin, who had carried out thousands of crosses, the use of sterility as a distinguishing character for species was an impossibility, and this fact was utilized by him in combating the criticism urged against the theory of natural selection, that it could not account for the origin of sterility by assuming that it was a factor in isolating species.

It has been only within comparatively recent times that an understanding has been reached as to what are the intimate results of sterility. It is true that Gärtner knew that the pollen of many hybrids was shrivelled and functionless, but farther than this, nothing was known of the condition of the spore-bearing and gamete-bearing parts; for the rôle of the pollen-tube, with the nuclei contained, and of the ovum in the ovary was as yet unknown and the discovery of the alternation of generations in the higher plants had not been made. Not until the reduction of the tetrads had been worked out was it possible to understand the failure of the hybrid to produce seed, or, if seed were produced, to understand why abnormalities occurred in the young hybrid plants.

We have spoken thus far mainly of the work of botanists, for the reason that little or nothing has been accomplished by zoologists until recently, which throws light upon the problem of sterility. It was known by Aristotle that species would cross and that the offspring varied from the parents in vigor and in other characters. If the etymologists inform us correctly, the word leopard, compounded of *Leo,* lion, and *Pardos,* panther, or tiger, points to a belief among the Greeks, that the leopard was a cross between the lion and tiger. The knowledge that captive animals bred only rarely, many not at all, and that even when mating occurred, the act was functionless and no offspring resulted, although the animals were apparently normal, is nothing of recent date. As to why offspring are not produced under these conditions, we are wholly ignorant. No one has determined whether the male actually conveys the fertilizing fluid to the female and if so, whether functional spermatozoa are present. It is known that in some cases, confinement of wild animals induces degeneration of the internal generative organs. Psychic causes, too, are undoubtedly present, inhibiting the mating instinct, but these factors are so subtile that they defy analysis. The data are familiar to every keeper of zoological gardens, and yet no attempt, to my knowledge, has been made to determine any of the details involved.

Several cytologists have examined the gonads of hybrid animals with a view to determining the condition of the sex cells. Thus, Guyer studied the crossed pigeons from the cotes of Professor C. O. Whitman at Chicago and found great abnormalities in the secondary spermatocytes, such as clumping of the chromatin, degeneracy of the cells as a whole, tri- and other abnormal mitoses. Spermatozoa were formed in many cases, but these cells were obviously abnormal and pathologic. The gonads of the mules obtained by crossing canaries and English goldfinches, siskins, bullfinches, etc., are degenerate, and in some cases which I have examined no trace of gonad could be found.

The cytology of the gonad of the mule obtained by crossing the mare with the jackass has been examined by H. E. Jordan who describes the testis as follows:

> The seminiferous tubules are lined with Sertoli cells, spermatogonia and a few primary spermatocytes in early stages. The nucleus of the latter appears to be in the spireme phase of the contraction stage and in process of regressive change. Mitoses are exceedingly rare and those

present are seen among the basal cells. Nothing corresponding to a secondary spermatocyte or a spermatid can be found, nor are spermatozoa anywhere present, either in the seminiferous tubules or the epididymis. The absence of spermatozoa explains why mules are infertile *inter se,* as also the fact that no issue results from a cross between a female horse and a male mule (the cross between a female mule and a stallion is known to have resulted in offspring).[2]

Aside from this study, and that of Guyer spoken of above, I know of no examination which has been made of the gonads of hybrid vertebrated animals. The conditions which I have found in canaries resemble closely those found by Guyer, in pigeons. The observations of Ancel and Bouin[3] on cryptorchid horses resemble to quite an extent, those by Jordan upon the mule testis.[4]

Hybridization experiments with lower forms of animals throw some light upon the behavior of the germ cells concerned in fertilization. Moenkhaus found that he could cross *Fundulus* and *Menidia,* two species of fishes, and obtain normal hybrids. Owing to the differences in size of the chromosomes in the two species, he was enabled to determine the fate of the chromosomes of the egg and of those of the spermatozoon and it was possible to follow them through the embryonic history, through the various mitoses of segmentation and later. Here, the chromosomes were in no way antagonistic and proceeded through the mitoses side by side.

Balzer[5] performed a series of very interesting experiments upon several species of echinoderms occurring in the Bay of Naples. He used four species, *Strongylocentrotus, Echinus, Arbacia* and *Sphærechinus,* making reciprocal crosses. Crosses between *Strongylocentrotus, Echinus* and *Arbacia* gave normal fertilizations, with no loss of chromatin in the earlier segmentation anaphases, and the plutei exhibited normal skeletons, except

[2] Whitehead, R. H., 1908, "A Peculiar Case of Cryptorchism and its Bearing upon the Problem of the Function of the Interstitial Cells of the Testis," *Anatomical Record* (Philadelphia, U. S. A.), Vol. 2, p. 177.

[3] Ancel et Bouin, 1903–4, *Journ. de Physiol, et de Path.,* T. 6, Nr. 6, 7. Also *Comptes Rendus,* T. 137, Nr. 26; T. 138, Nrs. 2, 3, 4.

[4] See Schwalbe, E. (Herausgeber), "Die Morphologie der Missbildungen des Menschen und der Tiere," Ein Hand- und Lehrbuch, Dritter Theil: Die Einzelmissbildungen.

[5] Balzer, F., 1909, "Ueber die Entwicklung der Echiniden-Bastarde mit besonderer Berücksichtigung des Chromatinverhältnisse," *Zool. Anz.,* Bd. 35, S. 5.

in one case. With *Sphærechinus* and *Strongylocentrotus* several chromosomes were eliminated in the anaphase of the first segmentation stage, which were excluded from the nucleus of the resulting cells, when the nuclear walls were formed. Correlative with this, the plutei showed abnormalities and the general resemblance was to the maternal species. Apparently here the case is different from that of Moenkhaus's *Fundulus-Menidia* hybrids, for the chromatin of the egg in part at least, is not adapted to association with that of the eggs of the other species. If this interpretation is correct, we may refer the abnormalities of the hybrid produced from the cross of *Sphærechinus* to the loss, during the segmentation stages, of chromosomes derived from the female. The analysis cannot be pushed farther back, in this case, for we are unable to understand why these chromosomes which are excluded from the reconstructed nucleus are "incompatible" with those of the egg-nucleus. Whatever the cause, it is probably similar to the agglutinization of erythrocytes, spermatozoa, bacteria and other cells in the fluids from other organisms or in artificial media. In this connection, it is interesting to recall that Guyer and Jordan found the abnormalities in the testes of hybrids appearing first during the synapsis period, when the chromosomes from paternal and maternal sources conjugate two-by-two, either end-to-end or side-by-side (probably side-by-side in chordates, according to the observations of Winiwarter). Recent study of spermatogenesis and oogenesis points to the conclusion that the maternal and paternal chromosomes remain distinct and more or less isolated from one another in the primary germ cells, from the time of fertilization until synapsis, and then for the first time are they intimately associated into pairs, as Montgomery suggested —a view which has been abundantly confirmed by Sutton, Stevens, Wilson, and a number of others. Here, then, would it be expected that incompatibilities, if ever present, would become apparent. If the phenomenon is of the same category as agglutinization, hemolysis and the like, it should be possible to render the sex-cells of one animal immune to the lytic action of those of other animals, on the principles of immunization and antibody development. In a case, however, where such a relation appears much more clearly, it seems that the phenomena are not of the same kind. I refer to the auto-immunity of *Cynthia*, where the eggs of a given individual of *Cynthia partita* cannot

be fertilized by the spermatozoa of the same individual. Morgan analyzed the phenomenon in the light of immunity and was unable to demonstrate a parallel between the *Cynthia* immunity and that in anti-body formation.[6] However, the case described by Morgan may not be equivalent to those of hybridization experiments, such as we have described.

Concerning the relation of the chromosomes to fertilization and subsequent condition of the embryo, Bataillon[7] derives certain evidence from his amphibian crosses for the conclusion that the number of chromosomes in the two parent species involved in the cross is of importance in determining the condition of the embryo resulting. Thus, when the number of chromosomes in the two species is the same, no embryo results, while crosses between species with different numbers of chromosomes lead to progeny. If this observation is true, it might be due to the fact that mainly, or only those chromosomes which are in excess of the number occurring in the species with smaller number of chromosomes and which do not pair up in synapsis with the chromosomes of that species, are functional in producing the embryo. Under these conditions, we should expect that the embryo would resemble the species with the greater number of chromosomes. However, this does not follow, inasmuch as Bataillon did not observe nuclear copulation, but rather a mode of artificial parthenogenesis is supposed to occur, the male element being wholly without effect in inducing fertilization and, therefore, the progeny would resemble the maternal species.

In 1906, Emil Godlewski, Jr., succeeded in obtaining a few hybrids between the sessile crinoid, *Antedon* ♂ and *Echinus* ♀, thus involving two classes of echinoderms, the Echinoidea and Crinoidea. The sperm exerted a marked inhibition of development as a whole and the hybrids resembled the maternal *Echinus*. This case is probably similar to the one described above where non-compatibility is evident between egg and sperm nuclei in fertilization. Godlewski did not examine the chromosomes with a view to determining their condition in the cells of the hybrids.

[6] Morgan, T. H., 1910, "Eggs of *Cynthia*, Immune to their own Sperm," a paper before the Society for Experimental Biology and Medicine, to be published in full in the *Journal of Experimental Zoology*.

[7] Bataillon, M. E., "Le substratum chromatique héréditaire et les combinaisons nucleaires dans les croisements chez les Amphibiens," *Comptes Rendus*, Paris, T. 147, f. 692.

Godlewski did not find it necessary to resort to artificial means in causing the spermatozoon of *Antedon* to penetrate the egg of *Echinus*, but by an ingenious method Loeb[8] was enabled to cause the egg of a member of one phylum to be fertilized by the spermatozoa from a member of a different phylum. Kupelweiser[9] afterwards applied Loeb's method to a cross between the mussel, *Mytilus* ♂, and the echinoderm, *Echinus* ♀, the method involving a subjection of the eggs to a hypertonic solution of sea-water, as in artificial parthenogenesis. Bataillon[10] believes that only artificial parthenogenesis is operative in this case, basing his conclusions partly upon analogous crosses in amphibians, where he has crossed *Triton* ♂ with the toad *Pelodytes* ♀, and observed that no sperm asters formed and segmentation proceeded without any participation on the part of the sperm nucleus.[11] Of course if Bataillon's contention is correct, the case is of no interest in the present connection, but if the two cases are not parallel, Loeb has overcome what we may grossly term sterility, by artificial means, by modifying the osmotic pressure and the permeability of the egg-membrane so that the spermatozoon of the foreign species may enter. Sterility here then may be due to purely mechanical factors. Yatsu has pointed out that the failure to procure crosses between the frogs *Rana sylvatica* ♀ and *Rana virescens* ♂ is due to the fact that the heads of the spermatozoa of the latter are too large to enter the eggs of the former. Here, again, a purely mechanical factor is involved.

While no experiments have been performed to my knowledge to determine whether a kind of acclimatization may be induced in hybrids, yet some experiments performed by botanists shed some light upon this point. Gärtner,[12] Wichura[13] and Nägeli[14] believed that fertility decreased in later generations, but Naudin,[15] C. C. Hurst[16] and others, including DeVries,[17] believe

[8] Loeb, J., *Roux's Archiv*, Bd. 26, Heft 3.

[9] Kupelwieser, H., *Roux's Archiv*, Bd. 27, S. 434.

[10] Bataillon, E., "L'imprégnation hétérogène sans Amphimixie nucléaire chez les Amphibiens et les Echinodermes (à propos du recent travail de H. Kupelwieser)," *Roux's Archiv*, Bd. 28, S. 43–48, 1909.

[11] Bataillon, E., "Imprégnation et Fécondation," *Comptes Rendus*, 11 Juin, 1906.

[12] Gärtner, 1849, "Bastarderzeugung im Pflanzenreich."

[13] Wichura, M., 1865, "Die Bastardbefruchtung im Pflanzenreich."

[14] Nägeli, C. v., 1866, "Botanische Mittheilungen," *Sitz. ber. der Münch. Akad. Wiss.*, 13 Jan., 1866.

[15] Naudin, Ch., 1869, "Nouvelles recherches," *Nouvelles Archives du*

that fertility increases, or, in other words the barrier, more or less perfect, between hybridization of the species involved, is gradually broken down. As Kerner[18] has shown, indeed, many hybrid plants are more fertile than the parent species and this is maintained and increased during future generations, so that the hybrids have replaced the parent species. There is, then, a basis for believing that a kind of acquired "congeniality" obtains, whereby the conjugating cells become more compatible, whatever this may ultimately involve. An interesting case was described by Gordon[19] where *Nicotiniana, Digitalis* and other hybrids are sterile *inter se,* but fertile with the parent forms. In the cross between the dog and the wolf, sterility begins, not in the earlier generations, but in later ones, according to the observations of Flourens, but as Darwin remarks, it is doubtful that this is due to increasing sterility because of crossing, but rather to confinement or, indeed, to inbreeding.

The students of plant cytology were the first to examine critically the structures concerned in reproduction in hybrids. Gärtner long ago observed the shrivelled pollen grains, as we have said before, but that was before the modern cytological methods came into use. Jančič[20] has contributed widely to this department of research. He observed that the number of pollen grains decreased in certain hybrid plants and that in the several species he examined, this numerical reduction occurred in approximate amounts to one fourth, one half or three fourths the average number of grains. Moreover, cytological examination of the anthers showed that many of the nuclei after reduction of the tetrads were atrophied, and the conclusion is obvious that herein lies the explanation of his numerical ratios mentioned above; for in some crosses, three fourths of the nuclei destined for the pollen (the daughter and granddaughter cells of the pollen mother-cell), or, in other words, three of the four tetrads, aborted, leaving but one to become pollen (hence the one fourth), while in other cases, two of the tetrads disappeared (two

Muséum a'histoire naturelle, Paris.

[16] Hurst, C. C., 1900, *Journ. Roy. Hortic. Soc.,* Vol. 24, p. 124.

[17] De Vries, H., 1903, "Die Mutationstheorie," Vol. 2, p. 66.

[18] Kerner, A. von, "Können aus Bastarden Arten werden?" *Oesterr. Bot. Zeit.,* Bd. 21, 1871.

[19] Gordon, D. A., 1862, *Mem. Acad. Stanisl.,* p. 228.

[20] Jančič, A., "Untersuchungen des Pollens hybrider Pflanzen," *Oesterr. bot. Zeitschr.,* 1900, Nr. 1, 2, 3.

fourths), so that one-half of the normal number of pollen grains appeared. Here, again, it is the period of synapsis or of conjugation of the maternal and paternal chromosomes (the stage corresponding to the gametophyte, where the chromosomes are reduced in number) where the effects of hybridization are evident.

Juel[21] has shown that the chromatin distribution in the nuclei of hybrids is irregular, corresponding to the conditions in hybrid animals described earlier in the present paper. The condition of the chromosomes during actual synapsis is such that it is impossible to observe their behavior directly and, doubtless, nothing could be learned of the ultimate cause of the irregularities through mere observation during these periods, even if the chromosomes could be more clearly followed. In such cases, it seems to me, we have fought the matter of sterility to its inner keep, and until experimentation comes to our aid, we shall be able to proceed no farther. "Über die Art und Weise, wie die Eizellen steril werden, haben wir keine erwähnenswerthen Angaben gefunden" (DeVries).

Several cytologists have taken advantage of the exhaustive studies of DeVries upon hybrids of the primrose, *Œnothera lamarckiana,* to study the cellular phenomena of crosses whose general features are well known. Thus, Geerts[22] has recently studied the partial sterility and the development of the embryosac of *Œnothera* and finds that there are no antipodal cells developed and that the endosperm forms from the pole cells. Sterility, says Geerts, is a matter of irregularities in the reduction division and therefore his observations tally with those, both plant and animal, spoken of above.

Gates[23] and Miss Lutz[24] have investigated the cytology of *Œnothera* crosses and of *Drosera* hybrids. Irregular distribution of the chromosomes obtained in the reduction division and these differences are correlated with the external characters of the crosses.

[21] Juel, H. O., "Beiträge zur Kenntnis der Tetradentheilung," *Jahrb. wiss. Bot.,* Bd. 35, 1900.

[22] Geerts, J. M., "Récueil Trav. Bot. Néerl.," T. 5, 1909.

[23] Gates, R. R., *Bot. Gaz.,* Vols. 46 and 48; *Science,* Vols. 27 and 30; *Archiv für Zellforsch.,* Bd. 3, H. 4, 1908–09.

[24] Lutz, Annie M., *Science,* Vol. 29, 1909.

Finally, Rosenberg[25] has invaded this fascinating field and studied the hybrid sundews exhaustively. The main results of his observations are similar to those given above in the case of the other workers. Rosenberg adopts the explanation of "Unverträglichkeit" (incompatibility) for the behavior of the chromosomes—a view which Tischler,[26] who speaks from much experience in the cytology of hybrids, believes to be inadequate, for the reason that, as Rosenberg as well as he himself shows, there are a few cases where typical embryo-sacs are developed and indeed the *anlage* of the young sporophyte may be found. "Die gewöhnliche Sterilität nicht in einer Unverträglichkeit der beiderelterlichen Chromosomen liegt."[27]

We are able to see, therefore, that sterility, as far as may be judged from studies upon the germ cells which have been made thus far, is a matter of the fundamental constitution of the organism. It concerns the bearers of hereditary traits, the chromosomes. All of the studies which have been made point to the conclusion that whatever may be its nature, there is an "incompatibility" existing between the chromosomes of individuals of different species or varieties. Tischler's contention seems to me to be ill-founded, for the cases where normal structures occur in the embryo-sacs of these hybrid plants are exceedingly few, and when we consider the observations of other workers upon plant material, and of the animal cytologists we find abundant reason to believe that the exceptions mentioned by Tischler may be better explained in another way. Moreover, we know nothing of the constitution of the nuclei of the cells of the young sporophytes, with respect to the mingling of maternal and paternal chromosomes. It may be, indeed, as Gates has suggested, that a condition of apogamy may obtain.

Undoubtedly the next few years will see many points as yet undetermined, brought into proper perspective and we shall be able to give a more complete account of the rationale of sterility.

MAX MORSE.

[25] Rosenberg, O., "Cytologische und morphologische Studien an *Drosera longifolia* by *rotundifolia*," *K. Vetenskaps Akad. Handl.*, Bd. 43, Nr. II., 63 S. Stockholm.

[26] Tischler, G., *Zeitschr. f. ind. Abstammungsl.*, Bd. 3, H. 3, 1910.

[27] Tischler, *l. c.*

NOTES AND LITERATURE

NOTES ON ICHTHYOLOGY

An elaborate and excellent monograph is the "Ichthyologia Amurensis," by Dr. Leo S. Berg, being a "Catalogue of the Fishes of the Amur River," entirely modern in its method, and very accurate in its details. Unfortunately, most of this admirable volume is in Russian, without résumé in any modern language. It is published by the Imperial Academy of Sciences at St. Petersburg, volume 24.

Professor T. D. A. Cockerell, of the University of Colorado, continues his very interesting and fruitful studies of the scales of fishes. In the *Proceedings of the Biological Society of Washington* (1910), he discusses the scales of the Cyprinoid and Clupeoid fishes. He shows that the American genera related to *Chondrostoma* are but two in number, *Orthodon* and *Acrocheilus.* The scales of the American species are less primitive than those of the old-world *Chondrostoma.*

In the study of the scales of *Leuciscus* and *Rutilus,* Professor Cockerell shows that none of the American species belong to either of these two genera, and none of them to the genus *Phoxinus.* For the American species called *Leuciscus,* the name *Richardsonius* of Girard should be adopted; and for the American species called *Phoxinus* the new subgeneric name *Margariscus* is suggested. The name *Myloleucus* of Cope is properly adopted for the American species hitherto called *Rutilus.* A new subgenus, *Temeculina,* is proposed for *Richardsonius orcutti.* The Japanese species called *Leuciscus* are not related to the European species, but approach more nearly to the American forms, perhaps entering the genus *Richardsonius.* Mr. Cockerell shows that the genus *Notemigonus* is well separated from the European genera *Abramis* and *Blicca.*

The scales of the herring-like fishes are also discussed. These show relatively simple and primitive structure.

The scales of the Atherinoid fishes show qualities more or less like those of the mackerels. In other papers published in the *Smithsonian Miscellaneous Collections,* volume 56, Mr. Cockerell discusses the scales of the African Mormyrid fishes and of the African Characins.

In the *Proceedings of the Royal Society of Victoria* (1909), Miss Ethel R. Morris and Miss Janet Raff discuss the structure of the little lancelet of the coast of Victoria, which they call *Asymmetron bassanum*. The generic name *Epigonichthys* of Peters has priority.

In the *Journal of the Royal Society of New South Wales*, Vol. XLI, Mr. H. C. Dannevig, of the Department of Fisheries, discusses the effects of the coastal winds of Australia on the abundance of fish in inshore waters. He shows that the relative abundance of many species in different places is due to the nature of the winds.

In the *Annals of the Carnegie Museum*, Volume V, Dr. Charles R. Eastman describes a new fossil shark, *Helodus comptus*, from Meadville, Pa.

In the *Annals and Magazine of Natural History*, Series 8, Vol. 4, Mr. C. Tate Regan describes a number of new species of fishes, mostly eels, from the South Seas and Australia.

In the same journal, Mr. Regan discusses the three-spined sticklebacks of the world. He finds those of the Atlantic coasts of Europe and America and those of the Pacific coast alike, including all the species of three-spined sticklebacks hitherto described under the name of *Gastrosteus aculeatus*, with the exception of *G. algeriensis*, which has a smaller number of vertebræ, 29 instead of 31 to 33. He also describes a species with a slender snout, from Rome, under the name of *Gastrosteus hologymnus*, and a new species, *Gastrosteus santæ-annæ*, from the Santa Ana River in California. This he regards as distinct from the naked specimens of *Gastrosteus* hitherto known as *G. williamsoni*, by the presence of 29 instead of 32 vertebræ. The specific distinction of *G. santæ-annæ* is very doubtful, but Mr. Regan is doubtless correct in saying that mailed, half-mailed and naked forms in Europe and America are the same species, those living in the sea being fully mailed, those living in fresh water mostly naked.

In the same *Annals*, Mr. Regan discusses the caudal fin of *Elops* and of other fishes. He finds the tail of *Elops* distinctly heterocercal, like that of some of the fossil forms of earlier periods. He also shows that the tail of *Fierasfer* is not gephyrocercal. In its general structure, it is like that of related forms, but the caudal fin has disappeared.

In the *Proceedings of the Zoological Society of London* for

1909, Mr. Regan discusses in detail the family of Anabantidæ.

In the *Archives de Zoologie Experimentale,* fifth series, volume 1 (1909), Dr. Louis Fage discusses in great detail the variations in the red surmullet of Europe. He finds that *Mullus surmuletus* is a form of *Mullus barbatus* somewhat less developed, so that the two species can not be maintained as distinct. If one is to give the right value to the variants of the surmullet, it is necessary to have not only a trinomial but a quadrinomial system of naming.

In the *Bulletin de la Société Philomathique,* 1909, Dr. Jacques Pellegrin discusses the minute catfish of the genus *Vandellia.*

In the *Proceedings* of the Seventh International Zoological Congress, Mr. Regan discusses the origin of the Chimæroid fishes. He regards them as derived from the same stock as the sharks, but more primitive.

In the said *Proceedings,* Mr. Regan discusses very fully the classification of the Teleostean fishes. It will be a long time before any satisfactory grouping of these animals can be made, but every analysis of this sort shows the importance of the problem, and the soundness of the American view, that a complete analysis of these forms must be made before any satisfactory synthesis is possible. To place groups together simply because we don't know how to separate them, does not form a classification of any permanence. A new order, Malacichthyes, is made for the genus *Icosteus,* and another order, Chondrobrachii, for *Podateles.* On the whole, this classification shows several points of advancement over any previously proposed, but there is plenty of room for doubt in regard to many of the adjustments.

In the "Scientific Investigations of the Fishes of Ireland," Volume 4, E. W. L. Holt and L. W. Byrne discuss the *Chimæras* of the Irish coast. These are three in number, *C. monstrosa, C. affinis* and *C. mirabilis. C. plumbea* and *C. abbreviata* are identical with *C. affinis.* A new species of *Rhinochimæra, R. atlantica,* is described. Of this genus, only a single Japanese species is hitherto known.

In the *Quarterly Journal of Microscopical Science,* volume 54 (1910), Professor J. Graham Kerr describes the development of the alimentary canal in *Lepidosiren* and *Protopterus.*

In the *Publications of the Department of State,* the International Fisheries Commission (David Starr Jordan and Edward Ernest Prince) have published the regulations, sixty-six in num-

ber, by which it is proposed to control the fisheries of the international boundary waters.

In the *Proceedings of the United States National Museum,* Dr. Jordan and William Francis Thompson describe a new species of deep-water sculpin, *Triglopsis ontariensis,* from Lake Ontario. The Lake Michigan form related to this, long since named *Triglopsis stimpsoni,* is also described and figured.

In the same *Proceedings,* Frank Walter Weymouth, of Stanford University, describes a collection of fishes from Cameron, Louisiana. One species, *Leptocerdale longipinnis,* is described as new. The three related species of this family, Cerdalidæ, are known from the west coast of Mexico.

In the "Smithsonian Report" for 1908, Dr. Theodore Gill discusses the variant forms of angler fishes, with figures of many species. He shows that the name *Lophiodes,* Goode and Bean, "Oceanic Ichthyology," p. 537, has priority over the name *Chirolophius.*

In the *Proceedings of the Portland Society of Natural History,* Vol. II, William Converse Kendall gives a list of the fishes of Labrador, as collected by the Bowdoin College Expedition of 1891. A check list of the species of Labrador contains seventy-three names.

In the *Bulletin of the Illinois State Laboratory of Natural History,* Professor Stephen A. Forbes gives a series of maps, showing the distribution of the fishes of Illinois in the streams of the state. The distribution of these fishes reflects, as Professor Forbes says, in uniformity and relative monotony, the features of the topography of the state.

In the *Philippine Journal of Science,* Vol. IV (1909), Mr. Alvin Seale describes a large number of new species of fishes from the Philippines, in addition to those named in the check list of Jordan and Richardson, published at about the same time in the same journal. Mr. Seale has had opportunities for making studies of the Philippine species such as have fallen to no other ichthyologist.

In the *Bulletin of the Bureau of Fisheries,* Vol. 28, are the proceedings of the Fourth International Fisheries Congress, held at Washington in September, 1908. Upwards of thirty papers bearing on fisheries are contained in this series, covering in some degree almost every matter of interest to fish culturists.

Notable among these papers is one by Dr. Theodore Gill, on a

plea for exact observation of the habits of fishes as against undue generalization.

Mr. L. F. Ayson discusses the introduction of American fishes into New Zealand, an operation which has been thoroughly successful. Most notable is the growth of the rainbow trout in the lakes of the northern island. Anglers are restricted to thirty pounds a day, and over twenty tons of trout have been taken out of two small lakes at Rotorua in one season. The rainbow trout is frequently taken from ten to twenty pounds or more in weight.

Mr. G. M. Dannevig discussess the success of the Norwegians in the planting of the fry of codfish in depleted waters.

Three papers, by S. W. Downing, Frank N. Clark and Paul Reighard, on the promotion of whitefish production in the Great Lakes, are especially important and suggestive. It is shown that with the adequate planting of whitefish eggs it would be possible practically to capture all the adult fish, and the natural spawning of the fish could be made a matter of no importance. This discussion looks forward to the time when the fishing season for whitefish will be largely identical with the spawning season; that is, in November, when the eggs of each fish thus caught will be preserved and hatched, and the young fish placed in the open water of the lakes. The whitefish ground is greater in Lake Erie than in any other of our American lakes. The plant of whitefish fry in Lake Erie now approaches one billion young fish per year, and, in spite of the enormous fishing taking place in that lake, the number of whitefish is increasing.

The following are the special recommendations of Mr. Reighard, and these should receive the most careful consideration from those interested:

1. It is recommended, as a result of the foregoing study, that the output of whitefish fry be increased as rapidly as possible, as affording the most certain means of increasing the whitefish production.

2. That an intensive plant of at least one hundred fry per pound of whitefish caught be made on depleted areas. (Lake Ontario and the southern waters of Lake Michigan are in need of especial attention.)

3. That a close season be observed during the breeding season of the whitefish as at present, but only for such waters as are not under federal control.

4. That commercial fishing with pound nets and seines be permitted in the waters of the Great Lakes during the breeding season of the whitefish wherever the state or national authorities are prepared to undertake to care for the spawn of the fish taken; the fisherman to be under legal obligation to permit the use of the fish taken by them for the purpose of spawn-taking.

5. It is suggested that central control of the fishing operations of the Great Lakes is highly desirable. Whether this is possible in American waters through federal control or through concerted action of the states is a question that can not be discussed here. A central control, under which fishing grounds should be leased and fishermen licensed, would, if properly administered, reduce the cost of fishing and make possible more extended artificial propagation. The central authorities should have power to modify the fishing regulations pending legislative action. Such a system might be made self-supporting.

6. The need of more exact knowledge of the habits of the whitefish and of all the conditions under which it lives is very evident. In the interest of the fisheries these matters should be subjects of investigations to be carried on under federal auspices, with suitable equipment and for a long period of years.

In another paper, President Jordan discusses the work of the International Fisheries Commission, outlining the proposed operations of Great Britain and the United States. This commission at that time had just been appointed.

John I. Solomon discusses a process for preserving the pearl oyster fisheries, and increasing the value of the yield of pearls. To this important contribution was awarded the prize of $100, by the New York Academy of Sciences.

Professor Shinnosuke Matsubara, of the Imperial Fisheries Institute of Tokyo, discusses the variant forms of the goldfish developed by Japanese artist breeders. These are illustrated by colored plates.

Professor Jacob Reighard, of the University of Michigan, gives a most valuable account of the nests of the horned dace, and of the methods by which the habits of fresh-water fishes can be effectively studied.

David Starr Jordan.

THE MAMMALS OF COLORADO

Colorado Mammals.[1]—About seven years ago I called on Mr. E. R. Warren at Colorado Springs, and saw his collection of mammals, then recently begun. It was a small affair, easily laid out on the parlor table. Since then, Mr. Warren has labored unceasingly, visiting many different parts of Colorado, and has accumulated an immense series of skins. The collection soon outgrew its original quarters, and is now housed in a special building, in numerous cabinets which are already overcrowded. While mainly a Colorado collection, it includes many species from other parts of the country, obtained in exchange. Mr. Warren has not only collected all these materials for taxonomic investigations, but has paid much attention to the habits of the animals, and in particular has secured a splendid set of photographs showing them in their native haunts. The logical outcome of all this excellent work, a book on Colorado mammals, has just appeared. It contains descriptions of all the species and subspecies known to inhabit the state, with numerous illustrations, showing the living animals and the skull of each genus. It is so far technical that it contains exact descriptions and all other details needed for precise classification and identification, but each form is also discussed in a popular manner, often with entertaining anecdotes. Heretofore the study of Colorado mammals has seemed too difficult for any one not a specialist, but with the aid of this book it is made easy for any intelligent person, or as easy as such a subject, from its nature, can be. The only regret I have about the work is that there is not more of it: I should have liked a chapter on fossil mammals (especially of the later periods), and one on parasites of mammals.

Apart from my great pleasure in the book itself, I can not other than regard the manner of its production as a good omen. Mr. Warren has lately been appointed honorary curator of Colorado College Museum, but he is essentially an amateur, in the best sense of that word. He resembles the numerous amateur naturalists of England, who have done so much for science; like them, he has labored for the love of the work, without recompense, and has shouldered the expense of publication, heavy as it must have been. The most modest of men, I fear he may resent being called a benefactor, yet it would be hard to exaggerate the benefit to the community which might come from an increase of the spirit he represents. T. D. A. COCKERELL.

[1] "The Mammals of Colorado," by E. R. Warren, G. P. Putnam's Sons, New York, 1910.